## *Conflict management in free-ranging immature rhesus macaques (Macaca mulatta).*

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# *Conflict Management in Free-ranging Immature Rhesus Macaques (Macaca mulatta)*

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*Thesis submitted in candidacy for the degree of Doctor of Philosophy*

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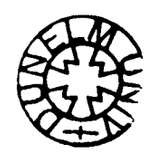

## *Abstract*

Group living primates utilise a number of characteristic post-conflict behaviours as a means of regulating the impact of escalated intragroup disputes. Although immature group members are typically implicated in disproportionate levels of aggression in many cercopithecine taxa, the conflict management abilities of young animals remain relatively unstudied as most previous investigations have focused solely upon adults or pooled data across age classes. This study therefore utilised a cross-sectional design to examine the immediate consequences of aggressive confrontations and the patterning of both affiliative and agonistic post-conflict interactions with former opponents and previously uninvolved bystanders, in free-ranging immature rhesus macaques (*Macaca mulatta*) at Cayo Santiago, Puerto Rico. Subjects of both sexes ($n$ = 108) and between 1 and 4 years of age were drawn from two social groups, upon which 451 pairs of 10-minute post-conflict and matched-control observations were collected over a 10 month period in 1996. These data were supplemented by 10-minute post-conflict intervals extracted from an additional 432 hours of continuous focal observations conducted upon a balanced subset of 36 juveniles, together with a total of 549 group-wide scan samples concentrating upon affiliative behaviour.

Involvement in aggression was found to have both social and ecological costs for former victims, which were subject to elevated rates of subsequent threats and attacks in the minutes following a conflict, a period in which they also spent more time in locomotion and less time upon feeding. Nevertheless the behaviour of aggressors was also affected, as contestants in both roles exhibited some degree of post-conflict elevation in self- (e.g. scratching) and object-directed activities (e.g. gnawing or manipulating) likely to be indicative of tension or anxiety, although these increases were often more pronounced in the recipient as opposed to the perpetrator of aggression. Affiliative reunions between former adversaries in the wake of aggression were demonstrable in even the youngest subject cohort and the patterning of these "reconciliatory" events was similar to that documented in previous work on adult macaques, with the context of the preceding conflict (over food versus of no discernible cause) and the quality of relationship between the protagonists (whether close kin or favoured affiliates, or not) significantly reducing or elevating, respectively, the likelihood that a reunion would take place. In the former case, variation in conciliatory tendency was also paralleled by a difference in the degree to which rates of self-scratching were elevated under post-conflict conditions, whilst in the latter case it was not - confrontations between close associates produced levels of scratching no higher than those after a dispute between less favoured affiliates. Immature subjects were also more likely to interact with certain other partner classes under post-conflict as opposed to baseline conditions. For example, there was a pronounced increase in affiliative contacts between former coalition partners following polyadic conflicts, these overtures typically being instigated by the beneficiary of support. Affinitive interactions between both aggressors and victims and previously uninvolved bystanders were also significantly elevated, being preferentially directed toward the contestant's close relatives and those of its opponent; the latter type of interaction appeared more frequent in the youngest subjects and partner selection was not merely a side-effect of proximity to members of the opponent's family. The degree to which kinship between former opponents, or with bystanders, influenced the likelihood of post-conflict affiliation was greater in female subjects, but the sexes behaved similarly in all other respects. Significant differences in behaviour between birth cohorts were also largely absent, although older immatures were more likely to "redirect" aggression toward third parties when victimised. These attacks against bystanders in the wake of conflicts were exhibited by both aggressors and victims, although aggressive responses were more likely when in the latter role. It is suggested that redirection by former victims may function predominantly as a signal to other group members, as these aggressive events were particularly likely to take place within view of former opponents and were associated with a high incidence of vocal threats; furthermore, redirection was associated with a significant reduction in the amount of aggression the subject subsequently received from others.

Immature rhesus macaques therefore appear to possess a rich repertoire of post-conflict behaviour, in many ways resembling that reported in previous studies based upon mixed-age subject samples. However, relatively small size and on average low rank may place greater constraints upon the behaviour of juvenile group members, which therefore may need to reach a certain age or size before fully expressing their potential. Further work is now needed to elucidate the functional consequences for immature contestants of the patterns of post-conflict behaviour documented, particularly those involving partners other than the former opponent.

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## *Author's declaration*

I confirm that no part of the material offered has previously been submitted by me for a degree in this or in any other University. If material has been generated through joint work, my independent contribution has been clearly indicated. In all other cases material from the work of others has been acknowledged and quotations and paraphrases suitably indicated.

## *Acknowledgements*

In this, as in any endeavour spanning several years, many people have played a part. Space and convention do not permit a full listing, and my apologies to any which may have been inadvertently omitted.

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# 1

## *Introduction*

Relationships between the members of primate social groups are inevitably a complex mixture of enmity and amity, as individuals attempt to further their own reproductive interests whilst simultaneously being reliant upon the tolerance and cooperation of others. In some cases conflicts of interest between group members are expressed as aggression, often with negative physical and social consequences. Behavioural means of forestalling, tempering and resolving such disputes are likely to be especially important for juveniles, whose small size and on average low rank render them particularly vulnerable to conspecific aggression; yet little is known about the development of conflict management skills in young primates. This thesis examines one aspect of the latter, documenting the aftermath of aggression and the post-conflict social responses of immature rhesus macaques (*Macaca mulatta*) of between one and four years of age, in a free-ranging setting.

This introductory chapter is divided into three main sections. In the first, a brief outline of theory concerning the causes and consequences of overt conflicts, and interspecific differences in the patterning of intragroup aggression, is provided. The second section reviews the variety of behavioural mechanisms which nonhuman primates have evolved to preempt and modulate escalated confrontations, as well as to cope with their potentially deleterious effects, with specific reference to the features exhibited by rhesus macaques and closely allied taxa. Finally, the third section introduces the special problems faced by juveniles in a world dominated by adults, and outlines the questions to be addressed by the thesis.

### *1.1 Cooperation and competition*

The majority of extant primate taxa live in cohesive social groups. A combination of ecological and social factors, predominantly enhanced abilities to locate and/or defend access to food resources against conspecifics (Wrangham 1980, van Hooff & van Schaik 1992, Drapier *et al.* 1999), a reduction in vulnerability to predators (Terborgh 1983, van Schaik 1983, Janson 1992) and, for females, protection against sexual harassment or infanticide by conspecific males (Smuts & Smuts 1993, Brereton 1995, van Schaik 1996), have been pinpointed as promoting group existence in nonhuman primates (although see te Boekhorst & Hogeweg 1994 and Hemelrijk 1996 for an alternative perspective). Offsetting such benefits are both direct and indirect costs (reviewed in Dunbar 1988 and Krebs & Davies 1993), notably the inevitable exacerbation of aspects of resource competition (see e.g. Whitten 1983, van Noordwijk & van Schaik 1987, Isbell 1991). Where the benefits of "joint action" outweigh such costs, then sociality

may evolve. Nevertheless, conflicts of interest between group members are an inherent accompaniment of group life (Alexander 1974, van Schaik 1989), for example occurring when the needs of two individuals cannot simultaneously be satisfied by limited resources such as preferred food, safe spatial positions, or mating opportunities. Less obviously, interests may also diverge when one animal seeks something from a conspecific who is unwilling or unable to comply with that expectation (Hand 1986, Mason 1993).

In many cases, the incompatible interests of groupmates may be resolved by resorting to aggression. However the threat, or use, of force is only one of several possible outcomes (Silverberg & Gray 1992, de Waal & Aureli 1997), avoidance or tolerance between individuals being alternatives. Traditionally, explanations have focused upon the fact that aggressive acts entail immediate *physical* costs, in terms of the time and energy expended, risk of injury or even death, and because participants may be exposed to greater predation risk. Game theoretic models therefore predict that the use of escalated aggression will be tightly constrained (Maynard Smith & Price 1973), and in many primates intense aggression and physical assaults indeed occur in only a small fraction of agonistic encounters (e.g. for data on rhesus macaques, see Bernstein & Ehardt 1985b). However, it is increasingly being recognised that where individuals reside in close knit societies, the use of both mild and intense aggression can also incur subsequent *social* penalties; the benefits of winning a fight may have to be traded off against the costs of creating an "enemy" within the group (de Waal 1989a). For example, direct retaliation against the perpetrators of aggression is a common phenomenon in certain taxa, and in some species individuals may preferentially join coalitions against adversaries which have frequently supported others against them (de Waal & Luttrell 1988, Silk 1992a). Targets of aggression and/or their allies have also been suggested to exert more indirect leverage, by subsequently victimising the relatives of their former opponents ("revenge": Aureli *et al.* 1992; "vendetta": Cheney & Seyfarth 1986, 1989). In recent years, the use of negative reciprocity as a framework to model the social constraints upon aggression imposed by such punitive responses has gained impetus (e.g. Clutton-Brock & Parker 1995, Matsumura & Okamoto, in press).

At the same time, unrestrained aggression may undermine and jeopardise vital cooperative relationships, reducing the tendency (and/or ability, if physical harm has been caused) of social partners to provide agonistic support or other favours in the future (de Waal 1989a). Primates are unusual in that a high proportion of aggressive disputes involve intervention by third parties (Harcourt 1992), and individuals rely heavily on coalition partners both in order to gain access to resources and to maintain rank within the group (see references in next section). Where a dominant's position depends upon agonistic support from a particular subordinate, intolerant treatment of this ally might result in a discontinuation of support, hence undermining the dominant's own position.

Paradoxically then, it is the need for allies in order to compete most effectively against other cliques in intragroup competition which also curbs the use of aggression. In the long term, the damage to relationships wrought by hostile acts may weaken bonds between group members and eventually compromise group integrity, thereby increasing vulnerability to the external threats posed by predators or rival social groups (de Waal 1992, de Waal & Aureli 1997).

The extent to which physically powerful or otherwise dominant group members can afford to use aggression against their inferiors has been linked to ecological and demographic factors. Early theoretical treatments suggested that the degree to which the cooperation of other individuals is needed, together with the options available to subordinates elsewhere in the population, interact to determine the distribution of power within social groups (Vehrencamp 1983, Hand 1986). Van Schaik extended these ideas in a socioecological model which took into account the abundance and distribution of resources and predators, in order to explain variation between primate taxa in the patterns of aggression and nepotism seen within groups (1989; with further development in van Schaik 1996, Sterck *et al.* 1997). According to this view, if groups form due to the need for cooperation against external threats such as predators or rival conspecifics, then dominant individuals derive direct benefits from the presence and actions of additional individuals. Groups are expected to be very cohesive if predation risks are high and a major factor promoting grouping; under these conditions it may be too costly for subordinates to leave if unsatisfied, dominants are free to exploit the advantages of their rank in within-group competition, and a "despotic" system ensues. In contrast, if high levels of between-group contest competition and the need for communal defense of food resources are the primary reason for grouping, and/or predation risks are relatively low, then subordinates have more option to withdraw their cooperation. Under these circumstances subordinates possess more leverage and dominants are forced to curtail aggression if others are to have sufficient incentive to remain with the group; hence relationships are likely to be more "tolerant" or, depending upon the within-group competitive regime, even "egalitarian".

Within the genus *Macaca* there is considerable variation between species in a cluster of behavioural characteristics concerned with conflict management, collectively termed "dominance style" (de Waal 1986a, 1989a, Thierry 1986). The covariation which exists between these traits is thought to derive from basic differences between despotic and egalitarian taxa in the intensity of aggression and degree of nepotism exhibited (Thierry 1990, in press; although see Hemelrijk 1999) thus ultimately being driven by socioecological factors, although phylogenetic constraints may also play some part (Petit *et al.* 1997; cf. Di Fiore & Rendall 1994). In a recent classification by Thierry (in press) extant macaque species were allotted to one of four modal sites on a continuous scale of social organization, ranging from despotic through more tolerant to egalitarian societies.

Rhesus macaques belong to the *fascicularis* phyletic group, alongside Japanese (*M. fuscata*), Taiwan (*M. cyclopis*), and longtailed (*M. fascicularis*) macaques (Delson 1980, Hoelzer & Melnick 1996). Of these, the former three were placed in grade 1 (the most despotic), while longtailed macaques were assigned to the second grade. In species such as these, dominant individuals exploit subordinates with impunity. Aggression is intense, tends to be unidirectional and directed down the hierarchy (Bernstein *et al.* 1983b, Thierry 1986, de Waal & Luttrell 1989, Chaffin *et al.* 1995), and conciliatory overtures following such confrontations occur at only low frequency (de Waal & Yoshihara 1983, Aureli *et al.* 1989, Schino *et al.* 1998). Relationships between unrelated group members are relatively intolerant; under most conditions a pronounced bias toward close kin exists in the distribution of affiliative acts and agonistic support (reviewed in Kurland 1977, Gouzoules & Gouzoules 1987, Bernstein 1991) as well as of reconciliation (e.g. Butovskaya 1993, Aureli *et al.* 1997). In contrast, the taxa placed in Grades 3 and 4 (a mixture of species from the *sinica-arctoides* and *silenus-sylvanus* lineages) are characterised by more tolerant or egalitarian societies, in which aggression is comparatively frequent but of low intensity, a relaxed dominance style is exhibited with a majority of aggressive acts inducing protests or counter-attacks, and reconciliation occurs following up to 50% of aggressive disputes (Thierry 1986, de Waal & Ren 1988, Abegg *et al.* 1996, Matsumura 1996, 1998, Petit *et al.* 1997). In these taxa, affiliation, support and reconciliation between unrelated groupmates are important and may approach the levels seen between kin.

## *1.2 Conflict management strategies in primates*

It is worth emphasizing that aggression is not an exclusively negative force but rather an adaptive and flexible component of primate behaviour, which can be used to negotiate relationships and manipulate social partners when the potential benefits make its use worthwhile (Dunbar 1988, de Waal 1992, 1996, Silverberg & Gray 1992). Threatened or actual violence may even produce socially constructive outcomes and be instrumental in maintaining cooperation; examples include the use of moralistic aggression among chimpanzees to promote egalitarian sharing of food, and the possible role of threats and punishment in the socialization of young rhesus monkeys by their older relatives (de Waal 1989c, 1992, Bernstein & Ehardt 1986). Nevertheless, the immediate effects of aggressive encounters typically involve not only the disruption of affiliative interactions between the protagonists, but also reductions in tolerance by the dominant party and an increased risk of further aggression taking place in the ensuing minutes (e.g. Aureli & van Schaik 1991b, Cords 1992). Foraging behaviour may be disrupted in the period immediately following a conflict, and thus ecological costs are also incurred (Aureli 1992, Castles & Whiten 1998a). Finally, involvement in aggression can be physiologically and psychologically stressful (e.g. Scallett *et al.* 1981, Levine *et al.*

1989; reviewed in Sapolsky 1998), and both these effects and those upon the patterning of interactions between former adversaries may persist over a period of days (Koyama 1997). As the effects of aggression are often detrimental - at least for one of the parties involved - group living primates employ a variety of behavioural mechanisms in order to forestall or modulate the expression of aggression, to improve their own competitive power and chances of success should an encounter take place, and to minimise the negative sequelae. The predominant means by which these effects are achieved are outlined below (see also Cords & Killen 1998 for a review which additionally provides analagous human examples).

*Behavioural conventions*

Game theoretical models predict that when the costs of escalated contests are high relative to the benefits of winning, conflicts of interest should instead be settled using conventions, with the behaviour of potential opponents reflecting a perceived asymmetry between the two (e.g. Maynard Smith & Parker 1976, Hammerstein 1981; reviewed in Reichert 1998). One example is the phenomenon of "respect for possession", whereby an animal typically refrains from contesting a non-divisible resource (such as a mate: Bachmann & Kummer 1980, or coveted food object: Thierry *et al.* 1989, Kummer & Cords 1991) if a rival's proximity to the resource is indicative of prior ownership. In the latter study, experiments on longtailed macaques demonstrated that the priority of access to a portable raisin tube normally enjoyed by the dominant member of a pair was constrained if the subordinate individual already maintained possession of the tube. The cost of aggressive interference by third parties appeared to be a factor favouring such respect as opposed to theft, as group members were more likely to be attacked when near to tube-owners which were screaming due to another's approach.

The phenomenon of social dominance itself (reviewed by Bernstein 1981, Drews 1993, Preuschoft & van Schaik, in press) provides an even more pervasive example. Where limited resources are economically defendable and can be sequestered by a single individual, contest competition is likely to ensue (Wrangham 1980, van Schaik 1989). By establishing pairwise dominance relations in which the subordinate party usually defers, the need to aggressively contest priority of access to essential resources on each and every meeting is obviated. Such a convention can be advantageous even for the subordinate, which thereby avoids the costs of contests which it may be likely to lose (Rowell 1974, Bernstein 1981), and in exchange for yielding gains peaceful coexistence in the group (and its associated advantages). Dominant group members gain preferential access to monopolizable resources such as food (van Noordwijk & van Schaik 1987, Dittus 1988, Barton & Whiten 1993) or water sources (Wrangham 1981, de Waal 1986c), and effective cover or safe spatial positions within the group (Janson 1990, Hall

& Fedigan 1997), and as a consequence high rank is often associated with greater reproductive success in female primates (e.g. Harcourt 1987, Silk 1993; although see Packer *et al.* 1995). Dominant males are often able to monopolize mating opportunities with fertile females and thus gain greater paternity (reviewed by Cowlishaw & Dunbar 1991, Ellis 1995), although the strength of this association is diminished under conditions in which many females are simultaneously receptive (e.g. larger groups, breeding seasonality: Paul 1997) or where males can use behavioural tactics to circumvent the constraints of low rank (see Pawlowski *et al.* 1998). Thus individuals often strive for high status (Walters & Seyfarth 1987, Chapais 1992), which may itself engender some competition, but on the whole the existence of this behavioural convention appears to manage aggression within and between primate groups; once dominance relations have been established between unfamiliar individuals, levels of aggression rapidly decline (e.g. Bernstein & Mason 1963; also reviewed in Mendoza 1993, Sapolsky 1993).

In the more "despotic" macaque taxa, dominance relations between group members are typically clearcut and one party may even formally signal its inferior status to a potential opponent (de Waal & Luttrell 1985, de Waal 1986a; see also Preuschoft 1999). These dyadic relationships are often reflected in linear or near-linear dominance hierarchies (in the latter case the overall hierarchy may be partitioned into several subgroups of individuals, within each of which the rank order is more linear), which in adult rhesus take the form of separate but partially overlapping rank orders for males and females (Sade 1967, 1992, Kaufmann 1967, Missakian 1972). In mature male macaques rank is largely dependent upon intrinsic attributes related to fighting ability such as age, size or strength, and in large groups upon length of tenure (Sugiyama 1976, van Noordwijk & van Schaik 1985, Manson 1998), thus fluctuating over time and following migration between groups. In contrast, female rank relationships are more dependent upon extrinsic factors such as support from relatives in alliances, are typically stable for prolonged periods of time in adults, and post-pubertal females "inherit" positions adjacent to their mothers and in inverse order of age (e.g. Datta 1983a, Chapais 1988, 1992; although see Hill & Okayasu 1995). This process of rank acquisition commences well before weaning (Berman 1980, Horrocks & Hunte 1983, Chapais & Gauthier 1993), although reversal with prospectively subordinate but much older and larger individuals may not take place for several years, when size differentials have been reduced. Dominance relationships of juvenile males whilst still within their natal group also depend to some extent upon maternal rank, especially where peers are concerned, although more recent work (reviewed in Lee & Johnson 1992, Pereira 1992, 1995) suggests that in fact relative age - and hence size - may be a more important determinant of male-male and cross-sex dominance amongst immatures (including in this population of rhesus; Kazem, unpublished data).

*Anticipating and preempting aggression*

Primates also appear to anticipate the outbreak of aggression, actively modifying their behaviour in several ways to minimise the likelihood of overt hostilities taking place. For example, in captivity both chimpanzees and stumptail macaques exhibit elevated levels of grooming prior to scheduled feeding times, a situation where contest competition and aggressive displacements are likely (de Waal 1989c, Mayagoitia *et al.* 1993, Koyama & Dunbar 1996). As grooming is effective in reducing physiological and behavioural indicators of tension (Terry 1970, Schino *et al.* 1988, Aureli *et al.* 1999), these alterations in affiliative behaviour appear to be an active strategy to dissipate tension and thereby avoid conflicts. In at least one case, these interactions have been shown to be effective in preempting aggression; in chimpanzees aggressive competition over food was more common during food trials which were not preceded by a "celebration", than in those which allowed the animals enough time to affiliate in the interval between first seeing and subsequently receiving the food (de Waal 1989c).

Another situation likely to provoke aggression occurs when stable captive groups are periodically crowded into familiar but smaller enclosures, given the enforced proximity and limited escape opportunities. In the short-term, primates appear to cope with this risk by simply limiting their overall levels of movement and social activity. Stumptailed, rhesus and longtailed macaques respond to experimentally induced increases in spatial density with greater avoidance behaviour and use of formal status displays, accompanied by increases in stationary huddling among relatives - perhaps a means of avoiding conflicts by "lying low" amidst the security of familiar partners (Demaria & Thierry 1989, Judge & de Waal 1993a, Aureli *et al.* 1995). Presumably as a consequence, the incidence of severe aggression may remain unchanged (Demaria & Thierry 1989, Judge & de Waal 1993a) or even decrease (Anderson *et al.* 1977, Aureli *et al.* 1995) at higher densities, although that of non-injurious forms which serve to space individuals and warn others to keep their distance may increase somewhat. Chimpanzees appear to adopt an even more effective inhibition strategy, in which the incidence of *all* forms of aggression actually declines under crowded conditions (Aureli & de Waal 1997). Longer term behavioural adjustment may additionally involve an active tension reduction strategy not seen in the short-term experiments. For example, rhesus groups held in high density conditions over a period of years exhibit higher levels of affiliative behaviour such as grooming and increased conciliatory reunions following conflicts compared with groups given more spacious enclosures (e.g. Novak *et al.* 1992, Judge & de Waal 1993b), whilst in intermediate density conditions individuals may simply shift patterns of affiliation so as to place relatively more emphasis upon nonkin partners (Call *et al.* 1996).

*Aggressive intervention in conflicts between others*

A distinctive feature of confrontations between conspecifics in many primate species is the high incidence of multipartite involvement (Harcourt 1988, 1992). Coalitions, in which individuals join in an ongoing dispute between others to aggressively support one or other faction, comprise the most common form (their patterns and usage being reviewed in Harcourt & de Waal 1992, Chapais 1995). When such cooperation between particular partners persists over the course of multiple conflicts, this is termed an alliance (de Waal & Harcourt 1992). Contestants often actively recruit the support of bystanders (de Waal *et al.* 1976, de Waal & van Hooff 1981), and there are indications that solicitation signals are directed preferentially toward those that can provide the most effective assistance - namely powerful group members which outrank the actor's current adversary (e.g. Silk 1999). Contestants thereby maximise their chances of a successful outcome to a conflict, while interveners use coalitions to influence the course of interactions between others to either their own or the recipient's benefit.

In female papionines interventions are weighted toward closely related beneficiaries, particularly where more costly forms such as defending victims against higher-ranking assailants are concerned (e.g. Walters 1980, Datta 1983b, Bernstein & Ehardt 1985a, Kaplan *et al.* 1987). Nevertheless nonkin may also be supported, although in these cases females consistently interfere in favour of the higher-ranking of two opponents - therefore typically supporting the likely winner - and rarely intervene in conflicts between more dominant group members (Pereira 1989, Chapais *et al.* 1991, Chapais 1992). Both this "conservative" pattern of support between nonkin, and the fact that young female macaques have been demonstrated to support even unrelated individuals in aggression against their own kin where those relatives are targeted for rank reversal (Chapais *et al.* 1994), suggest that these apparently altruistic acts are essentially selfish with immediate gains in terms of rank acquisition and maintenance. In these species males tend to intervene less frequently than females, and although factions do favour kin where available (e.g. Meikle & Vessey 1981, Silk 1992b) life-history and demographic parameters dictate that mature males ally predominantly with group members to which they are not related. Male alliances are shorter-lived and more changeable than the kin-based ones characteristic of females (van Hooff & van Schaik 1994), and in some species coalitions frequently contravene existing dominance relations, with subordinates combining forces to rout a male of higher status (e.g. Curtin 1981, Noë & Sluijter 1995). Again, rather than trading favours reciprocally, such support appears to be opportunistically donated in cases where cooperation potentially produces immediate dividends (e.g. in terms of access to oestrus females) for the actor (Bercovitch 1988, Noë 1990, 1992). Recent theoretical work also suggests that byproduct mutualism is sufficient to favour the evolution of coalitionary behaviour in general (Dugatkin 1998a).

*Mitigating or terminating conflicts between others*

Bystanders may also spontaneously intervene in a more impartial, or even peaceable fashion. Where successful, these interventions ameliorate the effects of aggression for the victim and/or result in the cessation of hostilities. In some cases, the mere approach of a more powerful group member is sufficient to induce the protagonists to break off a dispute and disperse (e.g. Gust & Gordon 1993). In several species, high-ranking males or females go further and sometimes intervene aggressively in a developing or actual fight without preferentially supporting one or other side, instead directing aggression at both contestants simultaneously, or sometimes briefly at each individual serially, until aggression ceases (rhesus macaques: Bernstein & Sharpe 1966, Boehm 1981, pigtail macaques: Oswald & Erwin 1976, chimpanzees: Boehm 1994). The resumption of hostilities then seems inhibited by the presence of the intimidating intruder, which may remain in the vicinity. These apparently protective actions toward vulnerable individuals are not necessarily biased toward related beneficiaries, and "policing" has therefore been interpreted in terms of suppression of the tension and disturbance created by overt conflicts, from which all group members may suffer and which may eventually jeopardize group cohesion. More recently, theoretical treatments have also suggested that arbitrating activities may be essentially self-serving, as impartial aggressive interventions evolve when winner effects are in operation (reviewed in Chase *et al.* 1994; see chapter 6 for further discussion). In this case the effects of winning disputes are self-reinforcing, and thus dominant individuals benefit if their interventions prevent competitors from gaining the advantages of a victory, which might otherwise lead to a string of successes and ultimately threaten the intervening animal's own position in the group (Dugatkin 1998a).

In contrast, in more tolerant taxa such as Tonkean and liontailed macaques (Petit & Thierry 1994a, in press) high-ranking males may intervene in a partisan fashion, but by directing friendly or appeasing gestures toward the aggressor in an ongoing confrontation. In this case, initiatives are more likely to benefit victims which are closely related to the actor. Thus these "peaceful" interventions have been interpreted as a less costly alternative to aggressive support for the victim, with the added advantage that the intervening animal does not thereby place itself in conflict, and perhaps endanger its own relationship, with the aggressor.

*Post-conflict behaviour*

Finally, if an aggressive conflict erupts a number of behavioural mechanisms are available to mitigate its negative effects and limit the likelihood of its recurrence. Of predominant interest have been the "reconciliatory" reunions exhibited by the vast majority of primate species studied to date, whereby former opponents interact

affinitively in the wake of aggressive encounters (reviewed in de Waal 1989b, 1993a, Kappeler & van Schaik 1992), and which have even been reported to occur between high-ranking members of different rhesus troops following intergroup confrontations (Judge & de Waal 1994). In the short-term these peaceful interactions between former adversaries have been demonstrated to restore tolerance by the dominant party to baseline levels (Cords 1992), and reduce the probability that the victim will be re-attacked or receive aggression from previously uninvolved bystanders (Aureli & van Schaik 1991b, Castles & Whiten 1998b). Behavioural and physiological indicators of fear and tension also decline more rapidly than they would otherwise (e.g. Aureli & van Schaik 1991b, Smucny *et al.* 1997, Das *et al.* 1998), and playback experiments have shown that avoidance responses by the former victim subside and the occurrence of subsequent affiliative interactions is facilitated (Cheney *et al.* 1995b, Cheney & Seyfarth 1997). Such benefits are also manifested over longer timescales; in Japanese macaques reconciliation in the minutes following a conflict is associated with the return of rates of aggression and grooming between former combatants to their baseline levels, when assessed over a 10 day period (Koyama 1997; although Silk *et al.* 1996 found no consistent long-term effect of reconciliation in female chacma baboons). By partaking in these friendly reunions, individuals appear able to minimise the physiological costs and social impact of involvement in aggression.

In the minutes following a conflict contestants may also engage in affinitive exchanges with previously uninvolved third parties at elevated rates. For example, former combatants may affiliate with their own relatives (Cheney & Seyfarth 1989, Judge 1991, Petit & Thierry 1994c), with close kin of their former opponent (York & Rowell 1988, Judge 1991, Das *et al.* 1997, Castles & Whiten 1998a), or with bystanders unrelated to either of the protagonists (de Waal & Aureli 1996, Das *et al.* 1997, Verbeek & de Waal 1997). A more complex form of kin-oriented affiliation, whereby the two sets of relatives contact each other in the wake of conflicts in which they were not themselves involved, has even been reported (Cheney & Seyfarth 1989). These contacts with bystanders have variously been interpreted as providing reassurance to distressed contestants (de Waal & van Roosmalen 1979), "substituting" for reconciliation with the opponent in cases where the latter is uninterested or otherwise occupied (Cheney & Seyfarth 1989, Aureli & van Schaik 1991a), or preventing the spread of aggression to the individuals which participate or other members of the contestants' matrilines (Judge 1991, Das & van Hooff, in press) - depending upon the subset of third parties involved and whether the initiative was taken by the contestant or the bystander. However, with the exception of one study on longtailed macaques (Das *et al.* 1998, Das & van Hooff, in press), which produced negative results concerning the specific hypotheses examined, few authors have explored whether or not any of these functions are fulfilled.

Finally, in some cases an aggressive act may result in a cascade of contentious exchanges. For example, in those species in which the constraints of a strict dominance hierarchy limit opportunities for direct retaliation against aggressors (which are usually more dominant individuals), recent victims may "redirect" aggression by attacking a lower-ranking third party (e.g. Scucchi *et al.* 1988, Aureli 1992, Aureli *et al.* 1994; in Japanese, longtailed and Barbary macaques, respectively). Such acts may serve to reduce the physiological costs of being victimised (Sapolsky & Ray 1989), can preempt further aggression from the former opponent or opportunistic attacks from bystanders (Aureli & van Schaik 1991b), and appear to change the former aggressor's attitude toward the actor, making the former more likely to grant reconciliation (Aureli & van Schaik 1991a). Intriguingly, a few studies have also found that victims specifically target close relatives of their former adversaries (Judge 1982, Aureli & van Schaik 1991a, Aureli *et al.* 1992), especially those which are younger, and hence more vulnerable, than the opponent itself. Kin-oriented agonism may even generalise beyond the original combatants, with one party's relatives subsequently supplanting (Cheney & Seyfarth 1999) or actively harassing members of the other's matriline ("vendetta": Cheney & Seyfarth 1986, 1989, Aureli *et al.* 1992). Anecdotal reports of retaliatory antagonism towards an aggressor's unrelated close associates also exist, with male savanna baboons threatening or attacking the female "friends" of prior male opponents (Smuts 1985), although this issue has not yet been examined in a controlled post-conflict study. Where these acts are perpetrated by victims and their allies, kin- or associate-biased retaliation might constitute a source of social leverage used to discourage future attacks from the same aggressor.

## *1.3 Conflict management in immature individuals*

Conflict management abilities are likely to be especially important for immature group members. Anthropoid primates are unusual in that somatic growth rates descend to modest values shortly after birth and remain suppressed until puberty (Watts 1986, 1990), and as a consequence juveniles are typically much smaller than mature conspecifics. Although tolerance for the behaviour of young infants is usually high in cercopithecine groups, this period of amnesty is short-lived, and the small size and on average low rank of immatures places them at a considerable disadvantage in competition. Juveniles are frequently the targets of aggression from older group members (e.g. Dittus 1977, Silk *et al.* 1981, Bernstein & Ehardt 1985b, Pereira 1988b), with more severe contact forms of aggression being directed disproportionately often at immatures in several species of cercopithecines (Bernstein *et al.* 1983b, Bernstein & Ehardt 1985c). At the same time small size and inexperience render youngsters vulnerable to a greater range of predators (Janson & van Schaik 1993), which therefore cannot simply avoid adult assailants and are particularly dependent upon good

relationships with older group members in order to remain near the safer central portion of the group (Pereira 1988a, van Noordwijk *et al.* 1993, Horrocks & Hunte 1993). It is also during late infancy and the prepubertal period that young individuals begin the process of rank acquisition, increasingly begin to instigate aggression themselves, and move from being the predominantly passive recipients of support to actively intervening in conflicts between others (e.g. Cheney 1977, Chapais & Gauthier 1993, Kazem 1993, Prud'Homme & Chapais 1996). Thus the need to deal effectively with aggression would seem to be at a premium during this life stage.

However there have been few systematic attempts to explore juvenile competencies and the ontogeny of conflict management skills. Overall, the behaviour of juvenile primates has received much less research attention than that of either infants or adults (Pereira & Altmann 1985, Walters 1987). As Pereira & Fairbanks (1993) have pointed out, the neglect of this phase is ironic since protracted development (including extended juvenility or delayed sexual maturation) is the life history feature which best distinguishes the order Primates among mammals (Harvey & Clutton-Brock 1985). In particular, we lack information about the post-conflict behaviour of young individuals, previous studies typically having excluded the younger juveniles and pooled the remaining immatures with adult subjects in analyses. Conciliatory reunions involving juvenile contestants have received some attention (Cords 1988, Cords & Aureli 1993, de Waal & Johanowicz 1993, Judge *et al.* 1997), although comparison of their incidence and correlates in immatures of different ages have generally not been a focus (with the exception of a study on young tufted capuchins by Weaver & de Waal, 1997). Other aspects of post-conflict behaviour, including the social and ecological consequences of aggression, affiliation involving individuals other than the former opponent, and aggression toward third parties, remain virtually unstudied in immatures. In addition, the above studies were all conducted upon captive animals and were often experimental, for example involving artificially provoked conflicts or the co-rearing of different species. Therefore this thesis aims to expand upon current understanding by instigating a controlled cross-sectional study of immature subjects, examining a range of characteristic behaviour patterns following spontaneously occurring aggressive conflicts (henceforth simply termed "conflicts"), in a free-ranging population of rhesus macaques.

The remainder of the thesis comprises a chapter covering general methodology, followed by 4 data papers and a brief general discussion chapter. The 4 data chapters are largely self-contained, each with its own introduction, methods and discussion. Although this leads to some overlap in places, the intention was to allow each chapter to be read independently. Firstly, Chapter 3 documents the occurrence of operationally defined reconciliation between former adversaries, as well as post-conflict affiliation between former coalition partners, and explores the correlates of variation in conciliatory tendency. In chapter 4 the immediate aftermath of aggression is considered, examining

behavioural indicators of tension, rates of subsequent aggression, and alterations to time budgets from the perspective of both the aggressor and the victim. The association between post-conflict rates of self-directed behaviour and conciliatory tendency in specific contexts is also explored. Next, chapter 5 investigates whether affiliative interactions with particular categories of bystander, including one's own relatives and those of the former opponent, take place at elevated rates under post-conflict conditions. Finally, chapter 6 documents aggressive responses of both the aggressor and the victim to the original incident, and explores whether "redirection" of aggression might function as a signal used to dissuade others from opportunistically attacking recent victims.

# 2

## *General Methods*

## *2.1 Study site and population*

### *2.1.1 Study site*

Cayo Santiago is a 15.2 hectare island situated approximately 1 km off the southeast coast of Puerto Rico (18°09' N, 65°44' W), consisting of two smaller islets (a large and small cay) connected by a narrow isthmus. The climate is subtropical, with average rainfall of 163 cm per annum and mean daily temperatures ranging from 23.8 °C in February to 27.1 °C in July (Kessler & Berard 1989). Vegetation on the island ranges from sparsely wooded areas to dense undergrowth, with periodically waterlogged mangrove areas on the northern shore and exposed cliffs on the eastern and southern shores.

The island supports a free-ranging colony of approximately 800 rhesus macaques (*Macaca mulatta*), all current individuals being descendants of the founding population of 409 individuals trapped in the Lucknow region of India and released upon the island in 1938; no stock has since been added except through births. The animals are provisioned with commercial high protein biscuits at a rate of approximately 0.23 kg/ individual per day, distributed once daily (usually at 07:15 h) at the food dispensers located in 3 quarter-acre corrals. Nevertheless the macaques also forage extensively, with an estimated 50% of feeding time being spent on natural sources of food (Marriott *et al.* 1986, Marriot 1988) - the highest figures typically being achieved by the lower-ranking groups or individuals, which are more often displaced from the corrals. Natural food items consumed include foliage, fruits and berries (e.g. coconut palm, *Cocos nucifera*; Florida fiddlewood, *Citharexylum fruticosum*), flowers (e.g. Chinese hibiscus, *Hibiscus rosa sinensis*; white cedar, *Tabebnia heterophylla*) and various insects, as well as the ingestion of soil, the latter thought to aid in management of enteric parasite load (Knezevich 1998). Available water is supplemented via the collection of rainfall in cisterns and piping of water to drinking basins located a few hundred metres apart. There are no natural predators on the island; the primary sources of mortality are starvation and injury (Berard 1990).

Intervention is usually limited to an annual trapping period between January and March, during which the new yearlings are assigned identification codes (ear notches, tattoos), blood samples are obtained for analyses of paternity based on DNA fingerprinting, and all 2-year-olds receive innoculations against tetanus. Periodically, entire social groups have been removed from the island in order to control population size and density; in

1996 this management procedure was amended to instead entail the annual removal of a proportion of the juveniles from each troop (usually 2-year-olds, randomly selected with respect to family membership). Census records have been kept continuously since 1956, with the result that detailed maternal genealogies and male migration histories are known for all individuals. Further information regarding colony history, and population demography and dynamics can be found in Rawlins *et al.* (1984), Rawlins & Kessler (1986), Sade *et al.* (1985), and Kessler & Berard (1989).

### *2.1.2 Composition of study troops*

At the time of this study, the population consisted of between 4 and 6 naturally formed social groups together with a band of extra-group males and a handful of more solitary males. Data were collected on two related social groups, the larger (R) varying in membership between 182-202 individuals, and the smaller (BB) between 56-94 individuals over the course of the study (figures include all immigrants which spent ≥2 consecutive weeks with a group). The age-sex composition of each study group is presented in Table 2.2. Group R had formed as the result of a fission event in 1985, whilst group BB subsequently fissioned from R in the period January-February 1996 (the course of fission being similar to that described by Chepko-Sade & Sade 1979, and Malik *et al.* 1985), with the partition being complete prior to collection of the main behavioural dataset presented here. The study troops were the second- and third-ranking of the 6 groups on the island, with group BB - which was both smaller and largely formed by the lower-ranking females from R and their offspring - being the more subordinate of the two.

At the commencement of research both troops were organized in a manner typical of wild macaques, comprising a stable core of adult females and their immature offspring plus a number of more transient non-natal male residents. A small number of mature natal males were also present at times, although in all cases these were individuals which had temporarily returned following their natal emigration and/or subsequent transfers between groups. Detailed genealogies containing information on both relatedness (along uterine lines) and maternal rank within cohorts, together with a list of non-natal male group members, are provided in Appendix A1-2. Matrilines in the study troops each contained a maximum of 3-5 generations. During the formation of group BB, 2 of the 3 extended matrilines contained in group R had divided, such that BB comprised 2 matrilines each of which was related to one of the lineages in the remaining portion of group R. Although the division into separate troops was complete by March 1996, in August of that year one family from group R - part of the 777 matriline, which had been partitioned during the fission - began to spend increasing amounts of time with group BB (which contained the remainder of their extended matriline, and in which they became the highest-ranking

family). During the study period a neighbouring group (S) also underwent a gradual fission, with the result that one family (869+) and two juvenile sisters (84c and 06d) from the splintering group spent periods of time attached to groups R and BB respectively. Given that troops R and S had both been the fission products of the same original troop in the mid-1980s, these immigrants were in fact distantly related to some natal individuals in groups R and BB, and as they appeared to be well integrated (and lowest-ranking) members of the study groups they were treated as temporary residents in analyses. These associations apparently dissolved several months after the conclusion of this study.

Rhesus macaques are seasonal breeders (Lindburg 1971, Drickamer 1974), with the mating season usually extending from June-November and the birth season from December-May at Cayo Santiago. Thus individuals can be classified into discrete birth cohorts, henceforth referred to using the common age of their members in June 1996, the midpoint of the main phase of this study. Exact birthdates (± 24 hrs) were also known for all individuals in the study groups. For the purposes of this study, the definitions of developmental categories provided in Table 2.1 were adopted, broadly corresponding to the age cohorts specified.

*Table 2.1.* Definitions of developmental categories adopted in this study.

| Category | Age/ yrs | Definition |
|---|---|---|
| Infant | 0 | The period between birth and weaning |
| Juvenile | 1-3 | Post-weaning until puberty |
| Subadult | 4-5 | Sexually mature, but has not yet attained physical maturity |
| Adult | ≥ 6 | Adult body size, weight and dentition begin to be attained |

Juvenility is usually defined as the period between the point when an individual is able to survive the death of its mother (and therefore is no longer physically dependent upon her) and the onset of puberty, whilst adolescence is the interval from the onset of puberty to the beginning of effective reproduction (Pereira & Altmann 1985, Walters 1987). In rhesus macaques menarche usually occurs at 2.5 years of age, females undergo their first ovulation and conception at 3.5 years on average, and typically bear their first offspring at 4 years. In males, testicular descent occurs between 3 and 4 years of age, and individuals are capable of producing fertile sperm, and progeny, by 4 years (reviewed in Bercovitch & Goy 1990). However maturity is not attained until individuals reach adult body size, which in sexually dimorphic species typically occurs later in males than in females, and may constrain male opportunities to obtain matings. Skeletal maturation followed by attainment of adult body size occurs by about 6 years of age in female

rhesus, and up to 2 years later in males (Rawlins *et al.* 1984, Turnquist & Kessler 1989). However, there may be substantial inter-individual variation in the ages at which the above developmental milestones are attained (Pereira & Altmann 1985, Bercovitch & Goy 1990). Thus, for example, all subjects from the cohort aged 3 years in mid-1996 were termed "juveniles", although one such female did give birth in the final month of the study, just before entering her fourth year.

*Table 2.2.* Composition of study troops R and BB (March 23 - December 22, 1996)†.

| Group R | | | Group BB | | |
|---|---|---|---|---|---|
| Cohort | Male | Female | Cohort | Male | Female |
| Infant* | 21 | 18 | Infant | 9 | 5 |
| Juvenile | 33 | 34 | Juvenile | 11 | 14 |
| Subadult | 8 | 15 | Subadult | 3 | 3 |
| Adult | 31 | 35 | Adult | 12 | 12 |
| Total | 93 | 101 | Total | 37 | 35 |

†Values presented are the median number of individuals present in any one week; group membership fluctuated over time due to births, deaths, immigration and emigration. Temporary immigrants have been included in these figures if they spent at least 2 consecutive weeks with the troop, although only individuals which remained for ≥25% of the main study period were treated as "residents" and used in analyses. *The infant category for group R additionally includes the first 7 births from the subsequent cohort, which occurred during the final month of the study.

## *2.2 Data collection*

### *2.2.1 Schedule*

Focal subjects were selected from the intact group R, and preliminary focal and *ad libitum* (dominance) data collected between 01 November 1995 and 08 January 1996. Morphometric measurements were obtained and focal sampling ceased between 09 January - 28 February 1996, the period in which both the fission which produced group BB and the annual cull took place. Preliminary inspection of data collected in the two months preceding trapping confirmed that no apparent changes in rank relationships amongst the remaining individuals within each group occurred as a result of these two events. Collection of behavioural data resumed several weeks after trapping had terminated; thereon observations were conducted on both group R and its daughter troop BB. To provide a consistent dataset only the latter behavioural data, collected 23 March - 22 December 1996, are analysed and presented here.

Behavioural observations were conducted between 0700-1630 hours (0700-1500 in the case of focal samples) with approximately 50% of each week devoted to collection of the

post-conflict / matched-control samples and group scan samples on affiliative behaviour, and the remainder to focal sampling. Within each behavioural dataset approximately equal proportions of observations were derived from birth- versus mating-season weeks. This balance was viewed as important, given that frequencies of both agonistic and affinitive behaviour may fluctuate systematically between seasons in seasonally breeding macaques (e.g. Wilson & Boelkins 1970, Teas *et al.* 1982, D'Amato *et al.* 1982), although patterns of post-conflict behaviour such as reconciliation may or may not be affected (e.g. Aureli *et al.* 1993 versus Schino *et al.* 1998).

Data were collected using a combination of written checksheets and dictaphone recordings, with events being timed to the nearest second using a digital stopwatch. Observations were later transcribed and entered onto computer spreadsheets.

### *2.2.2 Post-conflict / matched-control observations*

*Subjects*

Paired post-conflict (PC) and matched-control (MC) observations were collected on individuals aged between 1 and 4 years (juveniles and young subadults), in both study groups. Effort was made to obtain every individual within this age range, and all but 8 of the 116 available immatures were sampled as focal subjects. Following conflicts in which both initial participants had been immatures, selection of focal individuals was such that approximately equal numbers of samples were collected on aggressors and on victims, and the participant which had been sampled least frequently in previous protocols was favoured.

*Observation procedure*

Observations were based upon a method developed by de Waal & Yoshihara (1983). Spontaneous aggressive conflicts involving at least one immature individual (of between 1 and 4 years of age) were selected opportunistically, and commencing immediately after termination of the last agonistic gesture of the encounter a 10-minute focal sample (Altmann 1974) was conducted on one of the protagonists. In order to qualify as a "conflict" for this purpose the interaction had to meet a minimum intensity criterion, i.e. involve a lunge or greater aggressive act (see hierarchy of aggressive behaviours provided in Appendix B). Facial threats were counted only if accompanied by agonistic vocalizations from at least one participant. Apparently unprovoked submissive gestures (e.g. fleeing, screaming) were not counted as evidence of a "conflict". To control against inflated post-aggression affiliation frequencies created by participants which maintained contact before, during, and after the conflict, opponents were also required to have separated to beyond arm's reach (>0.6m) of each other. In practice, adversaries usually

dispersed to at least 2m following conflicts of this intensity. Finally, conflicts which commenced in the feeding corrals were not used, due to the difficulty of accurately recording all the measures outlined below under crowded conditions, and in order not to bias the sample toward conflicts initiated over access to protein biscuits. If the original incident flared up again within <30 seconds this was treated as the same bout of aggression (unless the adversaries had in the meantime engaged in an interaction defined as mutually exclusive, for example affiliation), and the PC sample would be restarted from this point. This ≥30-second definition of the inter-bout interval for aggressive events was also retained throughout the continuous data.

Information recorded concerning the initial conflict included: [1] the identities of initiator and recipient, and whether the initiating party was the one to aggress first ("aggressor"), or the non-aggressive actions of either this individual (which subsequently became the "victim") or a third party ("cause") instead provoked the other individual into aggression. [2] The sequence of actions and the aggression of highest intensity exhibited during the bout. [3] Whether the aggression was unidirectional or counter-attacks took place, and whether a clear outcome was achieved or the outcome remained undecided (i.e. clear submission by only one of the parties did not occur). [4] The identities of any supporters (defined as third parties which intervened aggressively in an ongoing conflict) or helpers (individuals which entered the conflict on behalf of one party with ambiguous or distracting actions, e.g. screaming or alarm barking while darting at the target, but without the use of active aggression), their order of intervention, and whether their participation prompted the target to terminate aggressive acts and/or to submit. All recruitment behaviour of participants, and its timing relative to any intervention by third parties, was also noted. Any individuals which intervened in an ongoing encounter using affiliative acts (such as placing an arm around or mounting one of the opponents), almost invariably directed toward the current aggressor, were also noted. [5] The identities of all individuals within a 5 metre radius of either contestant at the start of the conflict, classified into categories of ≤2m or >2 - ≤5m. Infant bystanders were excluded from this measure, due to difficulties in identifying these individuals with requisite rapidity at the start of the study. All bystanders which approached to within 5 metres of the conflict but did not otherwise participate in any way, and all those which the combatants themselves approached during the conflict, were additionally recorded (again divided into the ≤2m and ≤5m distance categories). [6] The apparent cause of the conflict, where discernible. Whenever participants were in possession of or consuming a physical resource at the start of an encounter, its presence was noted, as well as whether the resource was relinquished to and/or then utilized by the opponent. If aggressive acts seemed directed toward or resulted in the cessation of an ongoing social interaction between the recipient and third parties, the identity of this social partner was recorded, as well as whether or not the victor subsequently interacted affinitively with the latter. [7] Finally, the distance

between the subject and its initial opponent (and in polyadic events, its main opponent) at the termination of the conflict was noted. This proximity measure was split into the following categories: >0.6 - ≤2m, ≤5m, ≤10m, ≤15m, ≤20m, and >20m.

During the ensuing 10 minutes, the initiation and termination of all social interactions in which the subject was involved were recorded to the nearest second, together with the identities of actor(s) and recipient(s). All vocalizations (if clearly directed toward other individuals) and facial gestures were included. Operational definitions of the behavioural measures used are provided in Appendix B. All agonistic interactions were recorded in as much detail as specified above for "conflicts", although where such interactions took place within feeding corrals only the presence of the mothers of immature participants (rather than all individuals present) within ≤5m was recorded for social context, as the crowding which often occurred around feeding hoppers made the full measure difficult to obtain. Movement of the subject into and out of the corral, as well as within and beyond 2 metres of the hopper, was timed to the nearest second. Restricted *ad libitum* data on third parties were also collected whenever these appeared to cast light on a focal animal's behaviour. For example, if a subject (A) threatened individual B, who had just threatened A's sibling, B's original threat would also be recorded and integrated into subject A's sequential record. Additionally, all conflicts (defined as above) between third parties which occurred within a 10 metre radius of the subject (divided into ≤5m and ≤10m categories) were monitored, and the identities and intensity of aggression used by the opposing factions noted. Finally, self-directed behaviour (scratching, autogrooming, yawning and body-shaking) of the subject was recorded continuously, with the identity and activity of the nearest neighbour (and of the individual to which the subject appeared to be attending at the time, if different) also being noted.

After 60 seconds had elapsed, and at 1-minute intervals thereafter, point time samples were taken in which the subject's maintenance activity was noted (again, see appendix B for definitions). If the subject was within a feeding corral at this point, this location would be noted as well as whether or not it was within ≤2m of the hopper. Proximity data on the identities of the nearest neighbour and all other individuals within a 5 metre radius of the subject were collected on every second point time sample. Individuals were assigned to the following mutually exclusive distance categories: in contact, within arm's reach (≤0.6m), ≤2m or ≤5m of the subject. Where no animal was within 5 metres of the subject, the distance (m) to and identity of the nearest visible individual were instead recorded. Infants within proximity were additionally distinguished as being "on" their mother or other caretaker, versus present whilst not being carried.

A matched-control sample, on the same individual and of the same duration, was collected as soon as possible on a subsequent day. Ideally, the start of an MC observation should be similar to that of the corresponding PC in all respects except the

occurrence of an immediately preceding conflict; therefore the following conditions were imposed. [1] If the focal animal had been involved in an aggressive encounter in the 3 minutes preceding the start of a planned MC, the MC was postponed by 10 minutes or, more usually, to the following day. [2] To ensure that former opponents were "available" to interact, every effort was made to ensure that the inter-opponent distance category at $t$=0 in an MC matched or was within that recorded at the start of the corresponding PC. If the former opponents were separated by >20m at the start of an MC, they were nevertheless required to be within the same subgroup (defined as within a 40m radius) and within sight of the subject. [3] Most studies stipulate that matched control observations should be collected at approximately the same time of day as were PCs (as a way of ensuring that general group activity is likely to be similar in the two samples), and in this study all MCs commenced within ±40 minutes of the PC starting time. [4] However, in free-ranging populations diurnal patterns of group activity may vary markedly from day to day due to factors such as prevailing weather conditions (e.g. Troisi & Schino 1986) and the movements of neighbouring troops. Therefore MC observations were also matched with respect to the predominant climate state (presence / absence of heavy rain) and major group activities at the start of the corresponding PC. Any activity in which at least 25% of group members within a 40m radius had been engaged at the beginning of PC samples was noted (classified as either consuming chow, foraging / drinking, resting / grooming, play, or group travel). Conditions at $t$=0 in MC samples were required to match at least the major group activity and that in which the focal animal had been engaged (if different) for the corresponding PC, and preferably any additional minor activities as well. [5] During the mating season the older female immatures were monitored for signs of oestrus, assessed using two 5-point scales to rate the degree of coloration and oedema of the sexual skin, as well as presence of any vaginal plug of coagulated semen, and any obvious consort behaviour. If either the subject or its opponent were deemed to be in oestrus on the day a PC was collected, every effort was made to collect the MC on the immediately following day (subject to the above criteria), because social behaviour may change markedly over the course of these cycles. [6] Finally, a planned MC was not commenced if the subject was clearly asleep at the appointed time. If the above conditions were not met within 10 days, the PC sample was discarded.

If a subject became obscured from view during a PC or MC sample, the observation continued for the full 10-minute period while efforts were made to relocate the focal animal if possible. During this time, the subject's former opponent(s) would be kept in view, to check whether any interaction took place between the former adversaries. These samples were regarded as truncated at the point the subject had disappeared from sight, but could be utilised as "entire" in analyses of *reconciliation* as long as the opponent(s) had been continuously monitored during the subject's absence. For analyses of other

behaviour patterns truncated samples were included or excluded on a case-by-case basis, according to the conditions outlined in specific chapters.

*Samples obtained*

A total of 455 post-conflict observations were obtained, of which 14 were discarded because no matched-control was obtained within the following 10 days. The remaining 441 PC/MC pairs were contributed by 108 focal immatures (mean = 4.1 pairs per subject; range 1 - 12 pairs). No individual was sampled as a subject more than twice against the same initial opponent. Equal numbers of males and females contributed to the dataset, with the distribution of individuals sampled across age cohorts, and between the 2 study groups, reflecting the relative proportions of immatures present in each group (Table 2.3). Group R, which contained approximately 3 times as many immature individuals as group BB, therefore contributed roughly three-quarters of the subject pool.

*Table 2.3.* Age-sex distribution of individuals sampled in the 2 study groups†.

| Age | Male | | Female | | Group R | Group BB | Total *N* |
|---|---|---|---|---|---|---|---|
| 1 | 23 | (3.0, 1 - 6) | 21 | (2.8, 1 - 6) | 31.5 | 12.5 | 44 |
| 2 | 11 | (6.0, 1 - 10) | 11 | (5.6, 1 - 10) | 16 | 6 | 22 |
| 3 | 10 | (4.1, 1 - 11) | 13 | (4.8, 1 - 12) | 14.5 | 8.5 | 23 |
| 4 | 10 | (4.7, 1 - 10) | 9 | (4.0, 1 - 8) | 17 | 2 | 19 |
| Total | 54 | (4.1, 1 - 11) | 54 | (4.1, 1 - 12) | 79 | 29 | 108 |

†Half values take into account the fact that a handful of juvenile subjects transferred between the two study groups, partway through the study period (see section 2.1.2, above). Values in parentheses provide the mean number and range of samples per individual within each age-sex class.

In 34.2% of these PC/MC pairs the subject had been the initiator of aggression in the original conflict (aggressor) and in 44.2% the recipient of aggression (victim); the remainder were from conflicts in which aggression had been bidirectional. The role of the subject in the conflicts sampled, according to age-sex class of the subject, is provided in Table 2.4. The majority of starting conflicts were dyadic, with only 37.4% of pairs pertaining to polyadic conflicts. In 13 pairs, either the PC or the MC observation had been truncated before 10 minutes had elapsed.

*Table 2.4.* Role of subject in conflicts sampled to commence PC/MC pairs, by age-sex class of subject. A = aggressor, V = victim, B = bidirectional, Total = all PC/MC pairs.

| | Male | | | | Female | | | |
|---|---|---|---|---|---|---|---|---|
| Age | A | V | B | Total | A | V | B | Total |
| 1 | 15 | 40 | 13 | 68 | 10 | 36 | 12 | 58 |
| 2 | 31 | 21 | 14 | 66 | 20 | 29 | 13 | 62 |
| 3 | 15 | 15 | 11 | 41 | 25 | 28 | 10 | 63 |
| 4 | 21 | 12 | 14 | 47 | 14 | 14 | 8 | 36 |
| Total | 82 | 88 | 52 | 222 | 69 | 107 | 43 | 219 |

### *2.2.3 Focal observations*

#### *Subjects*

Focal animals were a subset of 36* juveniles, selected from the pre-fission group R and drawn equally from 3 birth cohorts (1-, 2- and 3-years) such that each age category contained equal numbers of males versus females, and individuals of high, medium or low maternal rank. After the fission event, approximately one third of these animals resided in the newly-formed group BB. The sample contained 2 pairs of maternal siblings. *One 3-year-old female subject (52a) died approximately halfway through the main study period and was replaced by a closely related female of the same age (93a) who, of the potential replacement individuals, was closest in maternal rank to the original subject. One 3-year-old male subject (54a) became a peripheral group member approximately two-thirds of the way through the study, and eventually transferred into another group (F). Although observations were continued following his transfer, only the samples obtained whilst still within his natal group (R) were utilised in analyses. Summary details concerning these 37 focal subjects are provided in Appendix C.

#### *Observation procedure*

Observations were scheduled so as to achieve an equal distribution over the four 2-hour time blocks between 07:00h and 15:00h, as well as over the 36 weeks of the main study period, for each focal individual. The sequence of animals observed was determined by randomly selecting a focal immature from those remaining to be sampled in that round and during that particular time block, subject to the constraint that no individual was to be followed more than once on any one day. Observations in which the focal animal was lost within the first 10 minutes were discarded; if the subject moved out of view at a later point then the sample would be interrupted until the subject could be relocated. A maximum of 10 minutes' search time was allowed before moving on to the next animal

on the list. In the latter event, the remaining minutes of the former observation would be obtained on the next possible day, ensuring that the continuation period fell within the same 2-hour time block as the original sample.

Observations consisted of 30-minute focal follows, the protocol being almost identical to that specified above for PC/MC observations. However, in these observations very brief interactions - such as brushing past another animal during travel - were not consistently recorded. Focal observations also differed from PC/MC sessions in that point time sample and proximity data were only collected at 5 minute intervals.

*Samples obtained*

A total of $n = 24$ samples (i.e. 720 minutes) were obtained per subject with the exception of female 52a, who died during the study ($n = 12$), and her replacement 93a ($n = 12$). Additionally, only the 16 samples obtained before juvenile male 54a's natal emigration from group R were utilised in the analyses presented here.

Aggressive conflicts occurring within these samples were treated as starting points from which 10-minute post-conflict intervals were then extracted. These marker conflicts commenced with the first aggressive bout of an observation, provided it was of at least threat intensity (see hierarchy of aggressive acts provided in Appendix B; thus the conflicts used were sometimes of lower intensity than those in the PC/MC dataset). Subsequent bouts of aggression which met this intensity criterion were used as markers only if they did not fall within 10 minutes of the preceding marker event, i.e. the post-conflict intervals extracted did not overlap. A small number of eligible conflicts in which aggression was directed against another species (e.g. a lizard, rat or bird), or in which vocal threats were directed into the distance with no individual being apparent as the target, were not utilised. For the purposes of the analyses presented here, only the 462 markers which were followed by a continuous 10-minute period of observation were retained, those falling close to the endpoint of a sample being discarded. A more detailed breakdown of the PC periods obtained for each focal juvenile is provided in Appendix C. Most analyses were further restricted to PC intervals following intragroup conflicts, those involving extragroup opponents being excluded.

### *2.2.4 Group scans*

*Subjects*

To obtain a measure of the preferred associates of each group member, scan samples recording proximity partners and affiliative behaviour were collected on the entire group. Scan data were not collected on group members less than 1 year of age, infants being excluded because during preliminary observations (conducted when the 1996 cohort were

still very young) these individuals proved difficult to locate and identify accurately with the requisite speed.

*Observation procedure*

During scan samples a circuit of the group was made in which the identities of all individuals located, and of any partners within proximity of 1 metre or engaging in affiliative contact (or non-contact play), as well as the nature of such contact (contact-rest, embracing, grooming, mounting, play), were recorded instantaneously for each group member located. In order to procure an even distribution of scans across the day and ensure the independence of these samples the scans were centred approximately on the hour, with consecutive samples being collected at roughly 2-hour intervals - a period during which all individuals, and usually the group as a whole, had invariably changed location. Thus a maximum of 4 scans were obtained from any one group in one day, data collection alternating between sets of scans which commenced upon even versus upon odd hours.

Samples were recorded using a dictaphone, and later transcribed. In practice, a complete circuit of the group was impossible to achieve virtually instantaneously, given the size of the study troops and the fact that group members might be widely dispersed, sometimes in dense cover. Therefore a maximum time limit was set for completing each scan (reflecting group size: 10 minutes for group BB, and 25 for group R) and, on the few occasions where an individual was encountered more than once during the same scan, only the information pertaining to an individual's first sighting was retained for analysis. Scans were truncated if the majority of the group commenced travel, or if a large-scale (e.g. inter-group) aggressive confrontation took place.

To minimise possible bias in the representation of individuals of differing age-sex class and status, the position from which sampling commenced (centre versus periphery of group) was systematically varied, care being taken to circle outside the group perimeter in order to also observe the most peripheral group members. Due to the degree of crowding often created next to the food dispensers in corrals, individuals located within ≤2 metres of the hoppers when first sighted were not recorded during scans; whilst the identities of those individuals actually in prolonged contact near feeders may still reflect tolerance and preferences for particular partners, the identity of *all* individuals within a 1 metre radius in such a situation was regarded as unlikely to reflect such choices.

*Samples obtained*

A total of 549 group scan samples were obtained, approximately evenly distributed with respect to time of day and between the 2 study troops (Table 2.5). The mean percentage

of non-infant group members located per scan was 65% in both groups (temporary immigrants as well as "residents" have been included in these calculations).

*Table 2.5.* Distribution of scan samples of affiliative behaviour obtained, by group and of day.

| Group | 0800h | 0900h | 1000h | 1100h | 1200h | 1300h | 1400h | 1500h | Total |
|---|---|---|---|---|---|---|---|---|---|
| R | 31 | 36 | 34 | 38 | 32 | 35 | 34 | 37 | 277 |
| BB | 31 | 37 | 33 | 35 | 30 | 35 | 34 | 37 | 272 |

### *2.2.5 Morphometric measurements*

*Subjects*

All measurements were obtained within a 3 week timespan, during the annual capture of the population (see section 2.1.1, above). A total of 92 animals were measured, the sample being limited to those individuals of between 1 and 4 years of age in the two study troops which had been earmarked for capture as part of the requirements of other ongoing research projects at the site; no 3- or 4-year-old females were available for measurement. Excepting 2 juvenile males which only later immigrated into group R, somatic measurements were obtained for all males aged between 1 and 4 years, and all 1- and 2-year-old females, which resided in groups R and BB during the study period.

*Data collection*

Subjects were immobilised with ketamine hydrochloride (Vetalar, Parke-Davis, Morris Plains, NJ), administered intramuscularly at a dosage of approximately 10 mg per kilogram body weight. All measurements were made on the right side of the body, with the animal in left lateral recumbency. Body lengths were assessed using sliding calipers fitted with a vernier scale accurate to 1.0 mm, measurements being made between easily palpable bony landmarks (cf. Turnquist 1984). The linear variables thus obtained included crown-rump length (vertex to caudal tip ischial tuberosities) and ulna length (olecranon process to tip styloid process ulna). These measures actually correspond to body segments rather than bone lengths *per se*, given that in living primates the overlying soft tissue is unavoidably included. Chest circumference was measured to the nearest 1.0 mm, using a standard tape measure. The tape was wrapped around the ribcage ensuring that it passed over both nipples, and adjusted until it was tight but not binding. To obtain mass, individuals were weighed on a digital platform scale accurate to 0.2 kg; for a subset of 2- to 4-year-old subjects more precise values obtained from a hanging balance accurate to 0.1 kg were also available. Finally, testicular volume (if descended) was estimated to the nearest half unit in the older immature males, using a Prader orchiometer

(Holtain Ltd., Crymych, UK). All body size measures were repeated 3 times, and the median value retained for analysis.

### *2.2.6 Ad libitum observations*

Records of dyadic agonistic encounters (overt aggression, approach-retreat, assertive gestures which produced a submissive response, and spontaneous submissive gestures such as grimaces; all defined as in Appendix B) involving group members were collected opportunistically. Interactions in which one individual single-handedly attacked, supplanted, or was avoided by multiple others were also noted, but no other forms of polyadic incident were included. The identities of the participants, direction of agonism and act of highest intensity, and outcome of the interaction would be recorded, along with the presence of any resource (food, water, play object, or social partner) and whether or not the latter was retained, transferred between opponents, used simultaneously, or simply abandoned. In addition, for all participants aged 4 years or under, presence / absence of their mothers within a 5 metre radius of the incident was recorded, classified as either ≤2m or >2m - ≤5m.

### *2.2.7 Census*

Records of group membership, transfers, births and deaths were noted during at least one circuit of each study troop per observation day. Where animals appeared to be transferring in / out of a group, a special effort would be made to census their position several times per day, until stable group membership was achieved. These records were supplemented by those maintained by the permanent staff at the site.

## *2.3 Data analysis*

### *2.3.1 Dominance relations*

The *ad libitum* data on agonistic interactions (above) were combined with equivalent data extracted from the focal and PC/MC datasets in order to define dyadic dominance relations and produce a rank hierarchy for each study group (see Appendices D1 and D2). Only approach-retreat, spontaneous submission, or assertive interactions (where accompanied by submission on the part of the recipient) were used in the latter two datasets, overt aggression being excluded because these acts were to be utilised in analyses of post-conflict behaviour. As *ad libitum* interactions had not been consistently collected on infant group members, dominance hierarchies were constructed only for residents of at least 1 year of age. Interactions between members of different study groups and those involving extragroup individuals were also discarded. A total of 10981

agonistic events (8807 from the *ad libitum* dataset, and 2174 from the focal and PC/MC data) were retained.

These were then cast into a dominance matrix, the individual which won more encounters being treated as the dominant partner in each dyad. For the few dyadic combinations in which both parties had spent time in both study groups, interactions were partitioned such that only those which took place in weeks during which the two individuals were co-resident in a particular group contributed to the matrix for that group. In effect, the dominance relationship within these dyads has been assessed twice, a necessary precaution given that relative status within a dyad may change following immigration into a new troop. The matrix manipulation program MatMan (version 1.0 for Windows; de Vries 1998) was then utilised to ascertain the optimal ordering of individuals, and to determine whether the overall hierarchy was significantly linear. This procedure has the advantage that tied (equidominant) and unknown (observational zero) dominance relationships can be taken into account when assessing the degree of linearity present in a hierarchy. However, due to limitations on the number of cells the program can handle (80 x 80), an overall result could not be produced for the larger group (R). Instead, the program was used to produce an optimal order within each of several overlapping subsets of individuals (for example all members of one sex, or of one age class) and the resulting partial orders then interleaved by hand to produce an overall hierarchy for the group. In analyses referring to the "relative rank" of contestants and particular social partners the actual dominance interactions for that dyad have been used to assign relative status, where available. Otherwise, and in all analyses referring to a contestant's "rank position", each individual's ranking was derived from its position within the overall hierarchy of immature group members.

### *2.3.2 Post-conflict behaviour*

Methods used to demonstrate the occurrence of characteristic post-conflict behaviours and which are common to chapters 3-6, together with basic statistical procedures utilised throughout the thesis, are outlined below. Additional procedures specific to individual chapters are contained in the Methods section of the relevant chapter, in which the following common procedures are only briefly summarised.

#### *Operational definitions of characteristic post-conflict events*

Several methods have been used to determine whether particular behaviour patterns occur earlier and more frequently under post-conflict than under control conditions. The 3 predominant methods differ in whether post-conflict observations are compared with specific single controls or multiple observations taken from baseline data, and in whether analysis is based upon only the first instance per observation of the behaviour of interest

or upon the rate of all such instances. Further details can be located in the original papers (PC-MC method: de Waal & Yoshihara 1983; time-rule method: Aureli *et al.* 1989; rate method: de Waal 1987, Judge 1991), and some discussion of their relative merits and weaknesses has already been provided by Kappeler & van Schaik (1992), Cords (1993) and Koyama (1997).

*The PC-MC method*

In order to demonstrate that a specific behaviour is more likely to occur under post-conflict conditions than at other times, this thesis relies mainly upon a derivative of the PC-MC method devised by de Waal & Yoshihara (1983). As this procedure relies upon the existence of a single "true" control for each post-conflict observation, particular care was taken to maximise the similarity between the starting conditions of paired post-conflict and matched-control samples (see previous section on data collection). In the following explanation the demonstration of post-conflict affiliation between the main protagonists in a prior dispute ("reconciliation") is used as an example, but the principles outlined apply equally to the investigation of other classes of partner (e.g. previously uninvolved third parties; chapter 5) and/or other behaviour patterns (e.g. aggression initiated; chapter 6).

The PC-MC method emphasizes the notion of a single critical social interaction occurring soon after termination of a conflict, and does not assume that the rate of further interactions between a given pair of individuals will necessarily also be elevated for a period of time once an initial post-conflict interaction has taken place. First, the occurrence and relative timing of the first affiliative interaction between former contestants in PC versus MC observations is ascertained. Each PC-MC pair is designated as either "earlier" (EP: defined as where the first act occurs earlier in the PC than in the MC, or only in the PC), "later" (LP: if the first act occurs earlier, or exclusively, in the MC), or "neutral" (if an act occurs in both PC and MC observations and latency to the first act is similar in both cases, or if the act does not occur in either the PC or the MC). Whilst the original method involved assigning each first act to the minute-block within which it fell in an observation, with a pair being categorised as "neutral" if the first acts in the PC and its corresponding MC fell within the same minute-block (regardless of whether the latency to such acts differed by 1 second or 59 seconds), I instead used a standard minimum difference in latency of 10 seconds, below which a pair would be identified as neutral. In analyses where the partner class of interest encompassed more than one individual, for example following conflicts where subjects had faced multiple opponents, only the first interaction with any member of the specified partner class was utilized per observation (cf. Das *et al.* 1997). Therefore in polyadic conflicts multiple subject-opponent dyads were not considered separately; such treatment may underestimate the occurrence of reconciliation, which theoretically need not occur

with each and every opponent. Following Aureli *et al.* (1989), PC/MC pairs were discarded if the subject was already involved in an affiliative interaction with its former opponent at the start of an observation, in order to avoid an artificial accumulation of reunions at $t = 0$ which had not actually commenced at that point.

A comparison of whether the proportion of earlier pairs (EP/T) is greater than that of later pairs (LP/T) is then conducted at the individual level, by means of a Wilcoxon signed-ranks test. The null hypothesis is that aggressive conflicts do not affect the probability of a specified type of social interaction occurring in the immediately following time interval, a situation which would lead to an approximately 50:50 distribution of earlier:later pairs per individual. Analysis at the level of the individual was deemed crucial, as individual behavioural strategies were the focus of interest; in many previous post-conflict studies data have been pooled and analysis conducted at the level of the PC/MC pair or the subject-opponent dyad. This constitutes pseudoreplication (artificially inflating the sample size, $N$, and the error degrees of freedom) which can lead to spuriously significant results, as well as failing to meet the assumption of independence of datapoints often required by the statistical tests employed (see Hurlbert 1984, Machlis *et al.* 1985, and Kramer & Schmidhammer 1992 for further discussion of these points). These problems are exacerbated when, as is often the case, data from the multiple subject-opponent dyads produced by each polyadic conflict are utilised separately. Unfortunately this point remains worth stating; although in recent years individual scores have increasingly been used as the basis of post-conflict analyses, publications nevertheless persist which pool data without appropriately modifying the interpretations then drawn from those results.

*Identifying the relevant observation period for analysis*

It is possible that basing the above comparisons upon data drawn from the entire (and arbitrary) 10-minute duration of PC/MC observations could lead to a genuine post-conflict increase in affiliation being overlooked, in cases where the baseline level of affinitive interactions with a particular partner class is itself high and any post-conflict increase is limited to only the first few minutes following a conflict (Aureli *et al.* 1989, Veenema *et al.* 1994). High baseline levels of first interactions are likely to occur in cases where a large number of potential partners is available in the class of interest (for example analyses concerning the partner category "bystanders"), and/or individuals exhibit a high motivation to interact sociopositively with those group members (e.g. in analyses of the subset of bystanders which were close relatives of the subject). Previous studies on several macaque species have demonstrated that the majority of any increase in affiliation (and in aggression initiated) with a number of partner classes does indeed occur within the first 0.5-3 minutes following a conflict (e.g. Aureli *et al.* 1989, 1997, Das *et al.* 1997), although first contacts which occur later on in a post-conflict observation may

still be functionally meaningful (see Cords 1993). Therefore, before concluding that an initial PC-MC comparison was nonsignificant, I also checked for the existence of any post-conflict increase limited to a shorter period of time immediately following conflicts, by conducting PC-MC tests upon information derived from only the initial portion of the paired observations.

In order to estimate the duration of the appropriate time "window" (if any) within which to repeat PC-MC comparisons, a variant of the time-rule method (Aureli *et al.* 1989, Aureli & van Schaik 1991a) was used. As with the PC-MC method, the time-rule is based upon the relative timing of the first affiliative act per observation, although in this case in the aggregate sample of PC versus MC observations. The procedure utilises a Kolmogorov-Smirnov two-sample test to examine whether or not the relative cumulative frequency distributions across time of first acts in the PCs and in the MCs differ significantly. If so, the time window (during which PC levels of first acts are elevated above MC levels) is taken to be the latency at which, in the aggregate sample, the difference between the two relative cumulative frequency distributions is first maximal. Although the original method again based analysis upon consecutive 1-minute blocks within each observation, I instead divided the observation period into blocks of 10 seconds (considered the smallest sensible interval, following Das *et al.* 1997), because the use of intervals as small as possible is advocated for the Kolmogorov-Smirnov test (Siegel & Castellan 1988). Once again, only the first affiliative interaction with any member of the specified partner class was utilised, per observation.

Therefore, in this study, the time-rule was used only as a simple means of objectively estimating an "appropriate" time-frame within which to perform PC-MC tests, but was not used to actually demonstrate whether a post-conflict increase existed in a specific behaviour. It has in the past been used for the latter purpose, and possesses the advantage that it does not rely upon a single control for each post-conflict observation (a procedure which is strongly affected by how "good" the match is between PCs and their corresponding MCs, as mentioned earlier). However, as a method of demonstrating the occurrence and frequency of reconciliation it has several shortcomings. Firstly, the analysis is conducted at the level of the behavioural event rather than on individual scores, and hence involves pseudoreplication. Furthermore, as Das *et al.* (1997) have already pointed out, the assumption of independence of datapoints is not met - the comparison is neither a truly paired nor unpaired one, given that some (but not all) PC/MC pairs contribute datapoints to both the PC and MC time distributions, and some subjects contribute multiple datapoints toward the PC, the MC, or both distributions. Finally, while very sensitive to differences in the shape of two distributions, the Kolmogorov-Smirnov test may fail to detect genuine PC increases on occasions where the PC frequencies of first acts are consistently greater than MC levels, but the MC time distribution largely mirrors the shape of the PC curve. In addition, in a comparison of

the two methods of operationally defining reconciliation, Cords (1993) suggested that the PC-MC method should be the procedure of choice for evaluating the occurrence and frequency of this behaviour, because the latter provided a better fit to results concerning the functional outcome of reunions than did definitions based upon the time-rule.

*Use of post-conflict data without control*

Another reason for using the time-rule is that it enables utilisation of post-conflict data without control under certain circumstances, thus allowing expansion of the PC/MC dataset via the addition of those PC observations for which no MCs had been obtained, as well as post-conflict periods extracted from the larger focal dataset. This is the purpose for which the time-rule was originally devised; if a significant difference between PC and MC conditions has already been demonstrated (for example via the PC-MC method) and the post-conflict increase can be localized to within a particular window of time, then any conflict followed by an affiliative act between former opponents within this initial time window can operationally be designated as "reconciled" (Aureli *et al.* 1989). Having derived the relevant time interval from the aggregate sample, the issue of whether its length could have been unduly influenced by the extreme behaviour of a few individuals can to some extent be addressed by subsequently testing whether the proportion of PCs within which at least one act fell within the initial window is significantly larger than the equivalent proportion of MC observations, at the individual level (cf. Aureli & van Schaik 1991a). Compared with alternatives, the time-rule provides a quick and easy means of locating any post-conflict interval within which the frequency of first acts is significantly elevated, and permits comparison with results from previous post-conflict studies which often utilise this method. In addition, examination of the time course of the decay in frequency of first interactions may itself be of interest. However, the demonstration of a significant difference between PC and MC distributions of (first) acts does not necessarily also imply that all (first) acts which occur within the specified time interval are meaningful (i.e. unlikely to have occurred in the absence of a preceding conflict). Strictly, only if the increase over baseline frequencies is also of sufficient magnitude (e.g. approaching 20-fold) is the latter assumption justified. Aureli *et al.* (1989) have themselves already alluded to this issue, in noting that the time-rule produces more errors of classification for subject (or partner) classes exhibiting relatively high baseline levels of the behaviour in question. However, examination of the time distributions produced in the following chapters (which admittedly consider only the frequency of first acts, rather than the overall frequency of interaction) suggested that in fact the magnitude of the PC increase *was* in most cases sufficiently large to warrant considering any act falling within the relevant PC time window as meaningful - and in those cases where baseline levels of first interaction were high and the former statement did not hold (see chapter 5), post-conflict data were not utilised without control and thus

this issue did not arise. Finally, post-conflict data obviously should not be used without control in comparisons between categories which may already differ in baseline rates of interaction (Aureli *et al.* 1989, 1997). For this reason the use of the time-rule operational definition, and hence of the expanded dataset of post-conflict intervals, has been restricted to certain within-individual comparisons (e.g. between conflicts in which the subject had been the aggressor versus the victim) but has not been used in comparisons of PC behaviour either between different subjects or within-individual but between different partner classes.

### *2.3.3 Statistical tests*

Most analyses were performed using SPSS version 4.0. Kolmogorov-Smirnov two-sample tests were calculated by hand, following the procedure outlined in Siegel & Castellan (1988).

Ideally, multivariate methods would have been used to simultaneously examine the effects of age, sex, rank, role in conflict, etc., upon the post-conflict behaviour of contestants. However, in many cases the data did not meet the assumptions of parametric tests (for example due to unequal variance between the categories compared for some variables, or because some subjects did not possess data for all variables of interest), and thus variables were analysed separately using nonparametric tests. Nevertheless mean values have been used when summarising data and in figures, both for clarity of presentation and in order to facilitate comparison with previous studies (which without exception present data in this manner despite often having performed nonparametric tests).

Unless otherwise specified, two-tailed tests were utilised throughout. Although in some cases clear predictions regarding the direction of any effect could be made on the basis of theoretical or empirical results from previous studies, it was not clear whether or not such predictions would necessarily generalize to the behaviour of immature animals. More importantly, the use of one-tailed tests is regarded as almost always inappropriate in most basic research because they make no allowance for the interest that the scientific community usually will have in results that run counter to prediction (Kimmel 1957, Lombardi & Hurlbert 1996). The only exception to this convention concerned the Kolmogorov-Smirnov tests described above. These were performed only after an initial PC-MC comparison had already established the direction of any tendency or significant result in the data, and therefore these tests were by definition one-tailed.

Following Mundry & Fischer (1998), in the few cases where sample sizes of individuals fell below those advocated in Siegel & Castellan (1988) for specific nonparametric tests,

the exact (rather than the asymptotic) variant of a test was utilised in order to guard against the possibility of spuriously obtaining a significant outcome.

The significance criterion was usually set at 5%, with values of $0.05 < p \leq 0.10$ being regarded as nonsignificant trends. Exact *p*-values have been provided in all cases, including for nonsignificant results (see Stoehr 1999). Unfortunately, the reliance upon nonparametric tests precluded the use of commercially available power tests (as advocated by Thomas & Jaunes 1996 and Milinski 1997, for example) to evaluate nonsignificant outcomes. However the sample size used (and some indication of effect size) is routinely provided alongside test results. In most cases where a nonsignificant, but relatively low, *p*-value has been obtained the sample sizes are sufficiently large as to warrant regarding the outcome as meaningful and acceptance of the null hypothesis as justified.

In order to control the probability of a type I error over multiple statistical tests, individual tests should each be evaluated against a more stringent significance criterion than the usual $\alpha$ level of 5%. The use of such correction factors does not appear to be a feature of the literature on post-conflict behaviour, although there are a number of common situations in which the same null hypothesis is effectively tested more than once and an adjustment of the significance criterion for such "families" of tests would therefore be advised (Chandler 1995). One example concerns the repetition of a PC-MC (or rate) comparison using only the data drawn from within a predefined initial time "window", after an original comparison using the entire 10-minute observation period has proved nonsignificant. A correction is applicable here because a significant result in *either* of the 2 tests would lead to rejection of the broader null hypothesis. The Bonferroni procedure would be excessively conservative in this case, especially given that the second test is not independent but is instead performed upon a subset of the data already utilised; thus the appropriate $\alpha$ level lies somewhere between $p \leq 0.05$ and $p \leq 0.025$, although the precise value to be used in such a second non-independent test does not appear to be easily ascertained. Erring on the side of caution, the criterion of $p \leq 0.025$ was therefore preferred for second tests of this type, with any *p*-values which fell between $0.025 < p << 0.05$ being interpreted as possibly significant but requiring further confirmation.

A second example concerns the use of multiple pairwise comparisons, for instance if the subject's role in the previous conflict is of interest and a total of 3 tests are performed in order to compare each of the classes "aggressor", "victim" or "bidirectional" participant against the others, sometimes with slightly different subsets of individuals contributing data toward the separate comparisons. In such cases Hochberg's (1988) procedure was used, which is less conservative than the standard Bonferroni correction and retains greater power in the individual tests. One starts by examining the largest of the *p*-values obtained in a set; if it is less than or equal to $\alpha$ (i.e. 0.05) then the null hypotheses of all the tests can be rejected. If not, then the $H_0$ of this initial test cannot be rejected, and one

moves on to compare the next largest *p*-value with the critical value of $\alpha/2$. If this *p*-value is smaller than or equal to the latter criterion, then this and the null hypotheses of all remaining tests with smaller *p*-values can be rejected. If not, this second hypothesis also cannot be rejected and one proceeds to compare the next largest *p*-value with $\alpha/3$, etc.. Throughout the thesis, corrections for multiple tests have been applied in situations corresponding to those described above. Where a *p*-value presented falls between $p \leq 0.05$ and a more stringent criterion applicable to that particular test, the result is highlighted and discussed separately in the text. Otherwise, all apparently significant *p*-values can be read as having further met any correction factor(s) applicable.

### *2.3.4 Analyses by group*

Primate groups which differ in size, composition, length of time that inter-individual bonds have been established, or spatial density sometimes exhibit variation in patterns of social behaviour, including post-conflict patterns such as reconciliation (see e.g. Call *et al.* 1996, Castles *et al.* 1996). In this study the 2 focal troops did not differ in the latter two respects (these being the two variables so far known to influence post-conflict behaviour), although they were of different size and may have differed in aspects of group composition (for example in the mean number of close kin possessed by each individual). Initial tests comparing PC and MC levels of the basic behaviours to be examined, with each of the major partner classes considered, were performed separately upon the 2 study groups. The direction of any effect was almost invariably the same in both groups, although comparisons were less likely to achieve significance within the much smaller sample provided by troop BB, and checks which required the more accurate scores of individuals possessing ≥3 eligible PC/MC pairs could not always be performed within the latter group alone. More importantly, the addition of data from group BB usually strengthened the significance of any result obtained within group R alone, and in over 35 tests performed in only 1 case was there any indication of a significant difference between subjects from the 2 groups in the degree of post-conflict increase exhibited (see Appendix E for a summary). Therefore, in the interests of retaining maximum sample size, and given that the issue of potential inter-group variation was not a focus of interest in this thesis, after checking that similar trends were present data from the 2 troops have been combined in the analyses presented.

# 3

## *Post-conflict affiliation between participants in the conflict*

### *Introduction*

In the wake of aggressive confrontations friendly reunions between former adversaries often occur, a phenomenon labelled "reconciliation" by de Waal & van Roosmalen (1979). In the years since this initial quantitative study on captive chimpanzees (*Pan troglodytes*) took place, many studies - which additionally control for expected rates of affiliation between the individuals concerned - have documented the ubiquity of such post-conflict rapprochement in a wide variety of primate species, under both natural and captive conditions (reviewed by de Waal 1989b, 1993a, Kappeler & van Schaik 1992). In fact in only two primate species examined so far, ringtailed lemurs (*Lemur catta*) and red-bellied tamarins (*Saguinus labiatus*), has this characteristic behaviour pattern failed to be operationally demonstrated (Kappeler 1993, Schaffner & Caine 1992). Comparable quantitative studies on domestic goats (*Capra hircus*, Schino 1998), spotted hyaenas (*Crocuta crocuta*, Hofer & East, in press) and bottlenose dolphins (*Tursiops truncatus*, Samuels & Flaherty 1997), now attest to the occurrence of similar post-conflict behaviour in a wide variety of socially living mammals. In some primate species, these reunions are marked by the use of special affiliative or sociosexual behaviour patterns largely confined to the post-conflict context (e.g. "kisses" in chimpanzees, de Waal & van Roosmalen 1979; or the "hold-bottom" ritual of the stumptailed macaque, *Macaca arctoides*, de Waal & Ren 1988). In these species, it is possible that the act itself may explicitly refer to the preceding aggression and affirm the cessation of hostilities, in the eyes of not only the participants but also of bystanders (de Waal 1989b). In other species, for example in many macaques, the behavioural components used may not be distinctive although relatively more intense or expressive forms of affiliation may predominate (e.g. Petit & Thierry 1994b, Abegg *et al.* 1996). Rhesus macaques are characterised as "implicit" reconcilers (de Waal & Yoshihara 1983, de Waal & Ren 1988), typically using ordinary components of the affiliative repertoire to achieve conciliation.

Although initially used only as a heuristic label without functional connotations, in recent years evidence of the benefits implied by the term "reconciliation" has accumulated. The predominant view is that cumulative bouts of overt aggression may damage the relationship between participants, an outcome which intervening post-conflict affiliation may avert by intermittently restoring the relationship to baseline levels (de Waal & van Roosmalen 1979, Kappeler & van Schaik 1992, Cords & Aureli 1996). In this view, reunions ultimately "repair" the damage wrought upon relationships. A rather different perspective has been outlined by Silk (1996, 1997, 1998), in which peaceful post-

conflict signals act simply as honest indicators that hostilities have terminated and of the actor's currently benign intent, thus facilitating the occurrence of affiliation between former opponents in the ensuing minutes. The two hypotheses are not necessarily mutually exclusive (see Cords & Aureli 1996 for further discussion). The occurrence of aggression is known to adversely affect interactions between the protagonists in a number of ways, at least over a period of minutes or hours immediately following the conflict (see chapter 4 and references therein for further details). Over prolonged periods of time such changes might sum to alter the nature of the relationship, if contestants continue to avoid each other and/or if an accumulation of short-term damage gradually undermines stable and predictable interactions between the individuals concerned. Although one study which examined longer-term effects in wild female chacma baboons, *Papio ursinus*, failed to find any consistent adverse effects of aggression upon social interactions between the former antagonists over the succeeding 10 days (Silk *et al.* 1996), a subsequent study of free-ranging Japanese macaques (*Macaca fuscata*, Koyama 1997) found that over a similar timeframe levels of aggression increased and grooming rates declined following unreconciled conflicts.

Furthermore, the occurrence of operationally defined reconciliation can be shown to alleviate these negative consequences, both in the short- and in the long-term. Following reconciliatory events, rates of self-scratching (taken to be an indicator of uncertainty or anxiety: Maestripieri *et al.* 1992) decline to baseline levels more quickly than they would otherwise do (in former victims: Aureli & van Schaik 1991b, aggressors: Das *et al.* 1998), as does heart-rate (Smucny *et al.* 1997, Aureli & Smucny, in press), suggesting a more rapid termination of the physiological and psychological stress provoked by the aggressive encounter. Tolerance of the former victim around resources by the dominant party increases to baseline levels (Cords 1992), and rates of both renewed aggression and aggression received from previously uninvolved third parties are significantly reduced (Aureli & van Schaik 1991b, Watts 1995a, Castles & Whiten 1998b). Experiments in which an affiliative vocalization by a former aggressor was played to its former target further demonstrated that avoidance responses of the victim subside, and subsequent affiliative interactions between the two parties increase, if such an apparently conciliatory event has taken place (Cheney *et al.* 1995b, Cheney & Seyfarth 1997). Finally, it has recently been shown that similar benefits are also manifested over longer timescales - reconciliation in the minutes following a conflict is associated with the return of rates of aggression and grooming between former adversaries to their baseline levels, when assessed over a 10 day period (Koyama 1997).

Despite these demonstrably beneficial effects, the majority of aggressive altercations often go unreconciled, at least over the post-conflict timeframes examined in most studies (typically less than 30 minutes). One reason may be that such interactions are potentially costly, especially for the victim; re-approaching a conspecific which has recently acted

aggressively is risky unless that individual's disposition has rapidly changed in the interim. Furthermore, cases of "false" reconciliation have occasionally been reported (de Waal 1986d, Cheney & Seyfarth 1990a) in which a former opponent is invited to approach, only to be re-attacked once it comes within range. Such acts of occasional deception can be compatible theoretically with even a system based upon honest signalling, provided they occur at only low frequency (Dawkins & Guilford 1991, Johnstone & Grafen 1993). It is also possible that dominant individuals have little incentive to participate consistently in conciliatory interactions - *unpredictable* granting of reconciliation might be adaptive, a way of ensuring that subordinate competitors are "kept on their toes" (cf. Miller 1997) and potentially very effective as a psychological stressor (see also chapter 4). Finally, in some species withholding of reconciliation might even be a deliberate act, used to punish others for the use of force perceived to be excessive or in some way unreasonable (de Waal 1996). Hence reconciliation should not be expected to occur following all disputes; as with any behaviour, the relative costs and benefits of engaging in post-conflict rapprochement need to be considered (Cords & Aureli, in press).

Reconciliation is therefore selective, and systematic patterns of variation in tendency to engage in these reunions can be discerned. For example, macaque species vary considerably in average conciliatory tendency (chapter 1; reviewed by Thierry, in press), consistent interspecific differences emerging despite the fact that many taxa have been represented by only one or two groups, and despite differences between studies in group composition and holding conditions. Within species, variation in conciliatory tendency between different classes of dyad has often been related to the presumed *value* (Kummer 1978) attached to specific types of relationship (de Waal 1986b, 1989a); conflicts occurring in more valuable relationships should be reconciled at higher rates as an individual risks a greater loss of benefits should the relationship dissolve. An elegant experimental demonstration of the importance of partner value was provided by Cords & Thurnheer (1993), in which captive longtailed macaques (*Macaca fascicularis*) were trained to cooperate on a simple task in order to obtain a coveted food. Following training reconciliation rates within these pairings increased threefold; higher rates of reconciliation appeared to be associated with the increased worth of partners able to cooperate in this fashion. Another example is provided by the common finding in many "despotic" cercopithecine taxa that kin reconcile more than nonkin, even when the greater baseline levels of affiliation between relatives are taken into account (reviewed in Veenema *et al.* 1994, Aureli *et al.* 1997). In these species, tolerance and agonistic support - particularly the more costly form of aid to victims - are strongly biased toward close relatives, and thus close kin are presumed to be particularly valuable partners.

However, the degree of *compatibility* (a term referring to the general tenor of social relations within a dyad: Cords & Aureli 1993, in press) between individuals may

influence the perceived accessibility of an opponent and hence will also affect the likelihood of reconciliation. For example, highly familiar group members which already share a history of positive interaction may find it easier to attempt reconciliation, whereas a less compatible opponent which might be more likely to react aggressively if approached would constitute a more risky proposition. Thus while partner value should influence the ultimate benefits of post-conflict rapprochement, partner compatibility may act as a proximate constraint influencing the costs of reconciling (Cords & Aureli 1993, in press). The latter may be a particularly important factor determining the post-conflict behaviour of immature individuals, which are often the victims of aggression from older conspecifics (see chapter 1) and may be reluctant to take the risk of initiating conciliation with much larger and higher-ranking opponents unless they happen to share a history of positive interaction. Unfortunately, in observational studies it is often difficult to differentiate the relative influence of value versus compatibility upon reconciliation frequencies. Indeed, the two may often go hand in hand; close kin are probably both more valuable *and* more compatible than other partners (Schino *et al.* 1998). However, in the experiment described above, Cords & Thurnheer (1993) were able to rule out increases in partner compatibility following training as an explanation of their results, which thus highlighted the contribution of partner value alone.

Reconciliation is the only post-conflict behaviour thus far to have been the subject of several studies specifically examining immature animals (longtailed macaques: Cords 1988, Cords & Aureli 1993; brown capuchins, *Cebus apella*: Weaver & de Waal 1997, in press), including three concerning juvenile rhesus (de Waal 1984, de Waal & Johanowicz 1993, Judge *et al.* 1997). However all the above studies were conducted in captivity, several were experimental in nature, and only one (Weaver & de Waal 1997) focused upon the natural ontogeny of conciliatory behaviour. Therefore the aim of this chapter was to document whether reconciliation occurred even in the youngest immatures (i.e. yearlings) and to evaluate which factors are associated with variation in conciliatory tendency, in a free-ranging population in which alternative options (such as effective avoidance of the former adversary) were also available. In addition, following polyadic conflicts the issue of whether subjects tend to engage in affiliation with other contest participants - namely their own coalition partners - at high rates was also examined. This phenomenon has occasionally been documented in studies utilising mixed-age samples (de Waal & Yoshihara 1983, Castles & Whiten 1998a), although the function of such contacts remains to be elucidated.

## *Methods*

Analyses were conducted upon 441 pairs of post-conflict (PC) and matched-control (MC) observations, collected on 108 focal immatures aged between 1 and 4 years. Further details concerning data collection and the distribution of these paired observations across age, sex and conflict role categories are provided in chapter 2. Not all PC/MC pairs were suitable for use in every analysis, and specific exclusions are outlined below.

I first examined whether former opponents were more likely to engage in affiliative interactions under post-conflict as opposed to baseline conditions. The range of behaviour patterns regarded as "affiliative" and hence scored in previous analyses of reconciliation varies widely, with some authors including even approaches into proximity whilst others count only interactions involving actual body contact (see summary in Casperd 1997). In this study the performance - even if by only one party - of any vocalization, facial gesture or act previously defined as affiliative in this species was included. This definition was adopted primarily to be sure of scoring *all* attempts at conciliation, in order to accurately determine when the very first overt interaction occurred and which individual took the initiative. In addition, definitions based solely upon the occurrence of physical contact between former rivals seem somewhat inconsistent, given that a brief touch by the former victim (regardless of whether tolerated, ignored or actively rebuffed by the aggressor) can count for more than, say, a facial signal or vocalization given by the aggressor, which might in reality carry more weight in terms of subsequent outcome. A list of the behaviour patterns defined as affiliative can be located in Appendix B. All nonaggressive and nonassertive body contact was included (e.g. resting in contact, embracing, grooming, mounting, play, muzzle contact or brushing past). Acceptable non-contact patterns included vocalizations such as girneys, low grunts and short coos, as well as gestures such as lipsmacking or play invitations - all of which have been predominantly associated with affinitive contexts and/or appear to signal positive intent in rhesus (see e.g. Hauser 1991, Hauser & Marler 1993, Kalin *et al.* 1992, Maestripieri & Wallen 1997, Silk *et al.* 2000). The gesture "present", which may be used to initiate affiliative interactions but is also used in submissive contexts (Maestripieri & Wallen 1997, Dixson 1998), was counted only if accompanied by other affiliative signals from at least one of the parties involved. Following Das *et al.* (1997), the proportion of first affiliative interactions which involved physical contact is also reported for the PCs, to provide some comparison with previous studies which based analyses solely on interactions involving contact. However, the figures provided tend to slightly underestimate the actual degree of contact achieved, because affiliation was defined using an interbout interval of ≥10 seconds. Thus the figures refer only to those contacts which occurred as part of, or within 10 seconds of, the very first affiliative act; in some cases individuals which did not use body contact during an initial bout of affiliation nevertheless then contacted each other in a later bout.

Analyses utilised a derivative of the PC-MC method (de Waal & Yoshihara 1983), in which the relative latency to the first affiliative action with a former opponent was assessed within pairs of PC and MC observations, and each PC/MC pair then designated as either "earlier", "later" or "neutral" (see chapter 2 for more detailed explanation of both this procedure and the following methods). The first affiliative act was defined as the first to occur with any partner belonging to the class of individuals under consideration, per PC or MC observation; thus in polyadic conflicts in which the subject had faced more than one opponent only the very first interaction with any opponent would be scored (likewise only the first interaction with any supporter would be counted in analyses of affiliation between coalition partners). PC/MC pairs in which one observation had been truncated before 10 minutes elapsed ($n$ = 13) were utilised in analyses of reconciliation if the subject's opponent(s) had been kept in view throughout the period in which the subject itself had not been visible. Otherwise, truncated pairs were utilised only when the duration of the shorter sample exceeded the time period required by the analysis (in cases where a period of less than 10 minutes was required), or if the first affiliative act with the partner category of interest had occurred in at least one of the observations before the latency at which the shorter sample terminated. A total of 3 truncated PC/MC pairs were therefore excluded. In addition, 2 PC/MC pairs in which the subject was already engaged in affiliation with its opponent at the start of the MC observation were discarded, in order to avoid an artificial accumulation of contacts "established" at $t$=0. However, these pairs could still contribute to analyses concerning post-conflict interactions between former coalition partners (below). A Wilcoxon signed-ranks test was then used to determine whether the proportion of "earlier" pairs (EP) was significantly greater than that of "later" pairs (LP), at the individual level.

The time-rule method (Aureli *et al.* 1989) was then utilised to identify whether there was any time interval immediately following conflicts within which any affiliative interaction taking place between former opponents could operationally be defined as reconciliation. This procedure has the advantage of enabling post-conflict data to be utilised subsequently without control, at least in cases where baseline levels of affiliation are not expected to differ systematically between the categories being compared. The length of any "time window" applicable was determined by using a Kolmogorov-Smirnov two-sample test to examine whether the relative cumulative frequency distributions across time of first affiliative acts in the PCs and in the MCs differed significantly. Once again only the first affiliative interaction with any member of the specified partner class was utilised, per observation. If significant, the time window was taken to be the latency (in 10 second intervals) at which, in the aggregate sample, the difference between the two relative cumulative frequency distributions was first maximal. In that case, reconciliation can be regarded as having occurred in a PC observation if the former opponents interacted affiliatively within this initial time window. In order to check that the result

had not been due to the extreme behaviour of a few individuals, I also examined whether the proportion of PC observations containing at least one affiliative interaction between former opponents within the initial time window was significantly greater than the equivalent proportion of MCs, at the individual level (cf. Aureli & van Schaik 1991a).

To examine whether former aggressors or victims assumed greater responsibility for initiating friendly reunions, only data pertaining to conflicts in which the direction of aggression had been unambiguous were utilised (i.e. counter-aggression had not occurred during the initial bout of aggression nor in any renewed aggression commencing within <30 seconds of the initial bout). The term *aggressor* refers to the individual which exhibited the first aggressive act of a conflict, whether or not this act had been provoked by other non-aggressive actions on the part of either the subsequent opponent or a third party (in such cases the latter individual was recorded as "causing" the conflict). The recipient of the initial aggressive act was termed the *victim*. Where an affiliative interaction between former adversaries took place, the party which had first approached (or which had directed the first affiliative signal, if the first gesture had taken place at a distance of >0.6m) was regarded as having taken the initiative. Given that observed patterns of initiative may differ depending upon whether only first acts falling within the operationally defined initial time window are used from the PCs, as opposed to all first acts occurring at any point within the 10 minute observations (Aureli *et al.* 1989), PC values have also been calculated based upon only those first acts falling within the relevant initial time window.

Nevertheless, a post-conflict increase in affiliation between former opponents might merely be the byproduct of a generally heightened tendency for subjects to affiliate with all group members, rather than being specific to former adversaries. In order to determine whether interactions involving former opponents were *disproportionately* elevated, the degree of post-conflict increase exhibited toward the latter was compared with any increase in affiliation exhibited between subjects and a standard "comparison group" of individuals. If the increase seen between former opponents is significantly greater than the increase with the comparison group of partners, we may conclude that the post-conflict attraction between opponents is in fact selective. The partner class "nonkin bystander" (i.e. individuals unrelated to either the subject or its initial opponent) was used for this purpose; this being the comparison group also used in chapter 5 to determine whether affiliation with other partner classes of interest (e.g. own kin, opponent's kin) was selectively increased in the aftermath of aggression. When comparing the incidence of post-conflict affiliation between different classes of partner (as here), or with the same partner class but between different focal subjects, it is important to use a measure which allows potential variation in baseline levels of interaction to be taken into account. The corrected conciliatory tendency index devised by Veenema *et al.* (1994; henceforth referred to simply as the CT) was used in such cases or, where a partner class other than

opponents was being considered, an analagous index (the corrected affiliative tendency: AT). In either case, the index for an individual with respect to a specific class of partner is defined as (E-L)/T, where E represents the number of "earlier" pairs, L the number of "later" pairs, and T the total number of eligible PC/MC pairs possessed. This measure is calculated per individual, irrespective of whether it was the focal subject or the social partner which initiated the first interaction.

It is still possible that former adversaries were more likely to interact during post-conflict observations simply because, as a consequence of having recently engaged in a conflict, contestants were more likely to be in close proximity at the start of PCs than at the commencement of MC samples. To control for this possibility, the PC-MC comparison was then limited to those pairs in which the distance between the focal individual and its initial opponent at the beginning of the MC had been within the same distance category (≤2m, ≤5m, ≤10m, ≤15m or ≤20m) as, or in fact less than, their separation at the start of the corresponding PC. Pairs of observations in which the inter-opponent distance had been greater than 20 metres at the start of both the PC and the MC were excluded, on the grounds that relative distance could not be assessed accurately in these cases. For pairs pertaining to conflicts in which the subject had faced multiple opponents, in this analysis only the first affiliative interaction with the *initial* opponent was utilised when classifying the relative latency to interact in PCs versus MCs, because the inter-opponent distances used referred to only the initial pair of combatants.

I then examined whether characteristics of the preceding conflict, such as the number of participants, intensity and direction of aggression used, or context of the dispute, were associated with significant variation in conciliatory tendency. Incidents in which more than 2 individuals were involved in aggression were defined as *polyadic*. Conflicts were partitioned into either *low intensity* (those involving threats through to lunges in the hierarchy of aggressive acts presented in Appendix B) or *high intensity* (those involving chases, manual contact, bites, or bidirectional aggression) encounters. Those in which the initial victim(s) and/or its supporters (if applicable) counter-aggressed against the initial aggressor were termed *bidirectional*. Thus the initial aggressor may or may not be the eventual winner in conflicts involving mutual aggression (although reversals in outcome were comparatively rare). Conflicts were classified as being over physical resources (*food*: forage, chow, water) if the aggression clearly concerned access to such a resource (e.g. the aggressor was attempting to prevent the victim from gaining access, or was attempting to take a resource held by the victim) and/or the loser relinquished part or all of the resource to its opponent. Aggressive encounters prompted by the victim's proximity to a third party or directly concerning access to a social partner - whereby the loser was forced to move away from and/or terminate interactions with a third party with which the aggressor then affiliated - were assigned to the category *social*. In the few cases where an incident concerned both types of resource it was assigned to the category

with which the aggression seemed most directly concerned; thus if a victim lost access to a water pool and in doing so broke contact with the animal next to it, and the aggressor immediately drank from the pool whilst ignoring the nearby third party, the encounter would be classified as *food* rather than *social*. Aggressive incidents in which no obvious context could be discerned were assigned to the category *none*. In order to ensure that clear and unambiguous categories were created, disputes in which physical or social resources were present but did not seem to be the cause of aggression - for example where a victim was foraging at the commencement of the encounter but the aggressor subsequently passed on without utilising this resource - were excluded from this analysis.

Next I explored whether attributes of the immature subject, namely sex and age, were associated with significant variation in conciliatory tendency. Given that post-conflict affiliation may be initiated either by the focal animal or by its opponent(s), the influence of these attributes was initially examined by restricting analyses to conflicts between opponents of the same sex, or age, respectively. The effects of sex or age disparity between contestants were subsequently investigated. In the subset of polyadic conflicts in which the focal immature faced more than one opponent the sex and age classification of the opposition was based upon the attributes of the initial opponent only, and therefore only the affiliative data pertaining to the initial opponent were utilised in assigning the relative latency of first interactions within PC/MC pairs. Subject *age* refers to the focal individual's cohort age, in years (see chapter 2). To examine at the individual level whether the age disparity between adversaries affected the likelihood that they would subsequently affiliate, the age difference between initial opponents was categorised as either low (difference of 0 or 1 year) or high (differing by ≥2 years). This particular division was chosen: [i] because it may be biologically meaningful - in juveniles from this population an age difference of 2 or more years corresponds to an approximate doubling of body mass and size (using a composite of linear measurements) relative to that of the younger individual (A.J.N. Kazem, unpublished data; see also Turnquist & Kessler 1989), thus such opponents may appear much more formidable in terms of size and strength. [ii] Preliminary inspection of pooled data revealed that mean conciliatory tendencies declined sharply if opponents were separated in age by ≥2 years (see Results). [iii] This division resulted in an approximately equal division of PC/MC pairs between the two categories to be compared.

Finally, conciliatory tendency was examined in terms of two variables reflecting the quality of relationship between immature subjects and their opponents: their degree of relatedness through uterine lines and their frequency of contact affiliation. At this study site networks of individuals known to be maternally related are extensive, but not all relatives are treated preferentially by the animals themselves. Previous studies examining the distribution of sociopositive behaviour and vocalizations in rhesus and Japanese

macaques have concurred in suggesting that individuals generally discriminate in favour of partners related at or up to the level of either avunculate or first cousins, the exact placement of the cut-off level of relatedness (beyond which rates of positive behaviour or attendance to others' vocalizations decline steeply) depending upon both the behaviour (e.g. costly agonistic support versus contact affiliation) and the species considered (Kazem 1993, Kapsalis & Berman 1996a, Rendall *et al.* 1996, Chapais *et al.* 1997). Therefore in this study opponents which were related at, or more closely than, the level of first cousins ($r \geq 0.0625$) were regarded as *close kin*. For the purposes of this analysis all other opponents, whether from the same extended matriline (i.e. distant kin) or from different matrilines or groups (assumed to be nonkin), were combined into the single category *other*. Data on affiliative interactions derived from scan samples of the entire group were used to classify the degree of "friendship" between contestants. For each group member the number of scans in which it had been observed in affiliative contact (play, allogrooming, resting in contact, etc.) with others, and the number of instances with each particular contact partner, were determined. Two individuals were considered to be *close associates* if at least one partner fell within the upper quartile of the other's distribution of contact affiliation scores. All remaining pairs of individuals were classified as *other associates*. Again, in the subset of polyadic conflicts in which the focal immature faced more than one opponent the relationship quality classification of the opposition was based upon the attributes of the initial opponent only, and therefore only the affiliative data pertaining to the initial opponent were utilised in assigning the relative latency of first interactions within PC/MC pairs.

The methods outlined above were then used to examine whether a post-conflict increase in affiliation took place between individuals which had supported one another in polyadic aggressive incidents, whether any increase observed was actually selective, and which party (donor or recipient of support) took the initiative. Both aggressive supporters (individuals which had aggressively aided one or other faction) and helpers (additional individuals which participated in the conflict in favour of one or other side, but used distracting or even submissive actions rather than exclusively aggressive acts) were counted for this purpose. One PC/MC pair was excluded from these analyses because the subject and its supporter were already affiliating at the start of the MC observation, and a further 2 pairs were discarded because one observation was truncated and the pair did not meet the criteria for inclusion.

All statistical analyses were conducted upon individual scores, and two-tailed tests were utilised throughout. The only exception concerned Kolmogorov Smirnov tests used to estimate the time window of elevation of PC affiliation, which were based upon first events occurring in the aggregate sample of observations and, given that the direction of the expected difference (i.e. a PC increase) had already been ascertained using the PC-MC method, were by definition one-tailed. Within-individual comparisons were

conducted using Wilcoxon signed-ranks tests, whilst those between individuals utilised Mann Whitney *U* tests. To maximise available sample size all individuals possessing eligible PC/MC pairs were utilised in initial comparisons. However, those which proved nonsignificant were also checked using more accurate individual scores, by restricting the test to individuals possessing ≥3 eligible pairs (or, in the case of within-individual comparisons of more fine-grained categories, to individuals possessing ≥2 eligible pairs of each subtype). In each analysis *N* refers to the number of individuals used, whilst the total number of PC/MC pairs contributing towards a particular test may be presented in parentheses or in the Figure legend. Values presented refer to mean (± SE) individual conciliatory or affiliative tendency scores, unless otherwise specified. The significance level was set at 5% unless a correction factor was in force, and *p*-values of between 0.05 and 0.10 are referred to as nonsignificant trends or tendencies. Where multiple pairwise comparisons pertaining to the same overall null hypothesis were performed (for example in comparisons between the conflict contexts food, social and none) Hochberg's (1988) procedure for adjustment of the significance criterion was used; cases where this more rigorous alpha level was not met have been highlighted in the text.

## *Results*

### *Post-conflict affiliation between former opponents*

Immature subjects were more likely to affiliate with former opponents under post-conflict conditions than baseline conditions, the proportion of "earlier" PC/MC pairs being significantly greater than that of "later" pairs at the individual level (19.7% EP versus 2.5% LP, of 436 pairs; Wilcoxon: $N = 108$, $Z = -5.35$, $p = 0.000$). Mean conciliatory tendency was 0.18 ($N = 108$ individuals), and 59.1% of the total of 88 first affiliative bouts observed in the PCs involved actual body contact. A significant post-conflict increase could be demonstrated even if a much stricter definition of affiliative interaction was employed, such that only those bouts in which the former opponents remained in contact for ≥ 5 seconds and/or exhibited bidirectional affiliative signals were scored (13.7% EP and 2.1% LP, of 436 pairs: Wilcoxon: $N = 108$, $Z = -4.96$, $p = 0.000$; mean CT = 0.14).

According to the time-rule, first affiliative bouts between former opponents occurred earlier in post-conflict periods. The relative cumulative frequency distributions of first acts in PCs and in MCs differed significantly (Fig. 3.1; Kolmogorov-Smirnov: $m = 87$, $n = 16$, $X^2 = 12.15$, $df = 2$, $p < 0.01$, 1-tailed), the maximal difference between the two distributions being located at <200 seconds. This "time window" was corroborated at the individual level, as focal subjects interacted affinitively with a former opponent within <200 seconds in a greater proportion of their PCs than of their MCs (PC: 0.164 ± 0.025,

MC: 0.007 ± 0.004; Wilcoxon: $N = 108$, $Z = -5.62$, $p = 0.000$). In combination, these methods therefore establish that former opponents affiliate earlier and more frequently following conflicts than under baseline conditions.

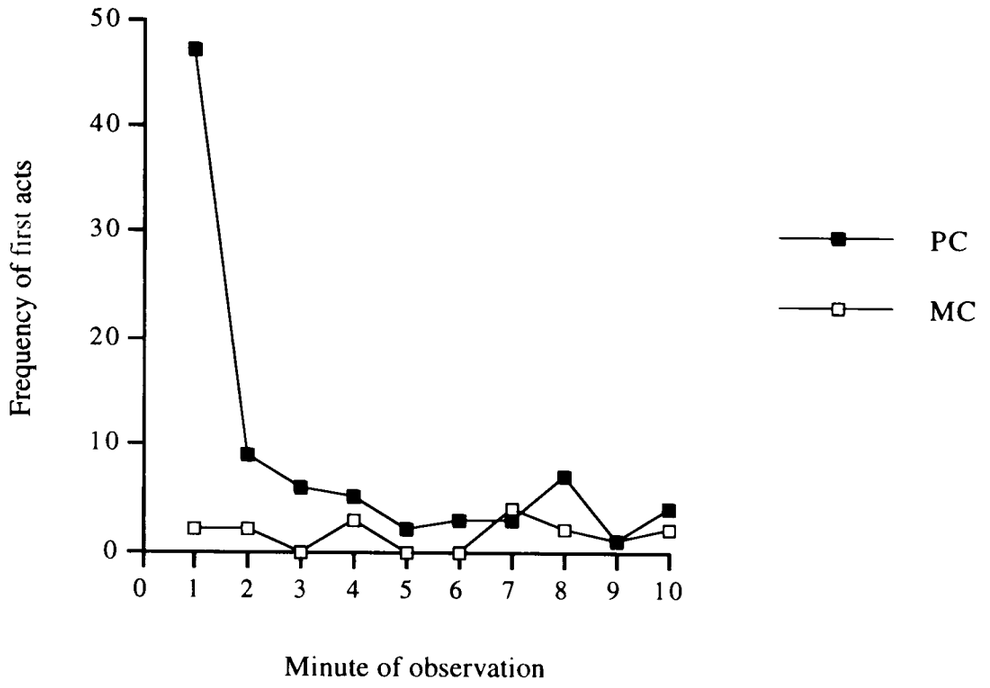



*Figure 3.1.* Distribution over time of first affiliative interactions between former opponents in aggregate post-conflict (PC) versus matched-control (MC) observations. Although the Kolmogorov-Smirnov test utilised 10-sec intervals, for simplicity results have been summarised using 1-min intervals in this and subsequent figures. From 436 PC/MC pairs.

*Selective attraction*

Nevertheless, the post-conflict increase in affiliation demonstrated above might be merely the byproduct of a generally heightened tendency for subjects to affiliate with all group members, rather than being specific to former opponents. In fact, focal individuals exhibited a post-conflict increase in affiliative interactions with all partner categories tested thus far (chapter 5), including even third parties unrelated to either the subject or its initial opponent (18.4% EP and 10.9% LP, of 423 pairs in total; Wilcoxon: $N = 107$, $Z = -2.61$, $p = 0.009$). Further information regarding the characteristics and distribution over time of first PC affinitive interactions between subjects and nonkin bystanders is provided in chapter 5. The tendency to affiliate with former opponents in post-conflict situations was, however, increased to a significantly greater degree than was the tendency to affiliate with nonkin partners ($CT_{oppt} = 0.18 \pm 0.03$, $CT_{nonkin} = 0.08 \pm 0.03$; Wilcoxon: $N = 107$, $Z = -2.37$, $p = 0.018$). Thus we can conclude that the post-conflict attraction seen between immature individuals and their former opponents is selective.

*Inter-opponent distance*

There were 343 eligible PC/MC pairs in which the distance between the focal individual and its initial opponent at the beginning of the MC had been within the same distance category (≤2m, ≤5m, ≤10m, ≤15m or ≤20m) as, or in fact less than, their separation at the start of the corresponding PC. Within these, the proportion of earlier pairs was still significantly greater than that of later pairs (17.8% EP and 2.6% LP; Wilcoxon: $N = 100$, $Z = -4.78$, $p = 0.000$). Therefore the constraint of MC inter-opponent distance upon opportunity to affiliate had not been responsible for the increased affiliation observed between former adversaries under post-conflict conditions.

*Initiative to affiliate*

To examine whether former aggressors and victims differed in their propensity to initiate affiliation with a previous opponent, comparisons were restricted to the 346 pairs in which aggression in the conflict had been uni-directional (i.e. excluding those involving counter-aggression). Of 53 first affiliative events which occurred between former adversaries within the initial <200 second time-frame following unidirectional conflicts, 30 (56.6%) were initiated by the former victim. If all first acts which took place at any point within the 10 minute duration of these unidirectional PCs were counted, 61.1% of 72 events were initiated by the victim. Thus it is possible that there is a slight tendency for victims to take the initiative. Only 14 cases of (first) affiliation between former opponents took place in the matched-control observations of unidirectional PCs; exactly half of these events were initiated by the former victim.

***Characteristics of the conflict***

*Conflict context*

The likelihood that post-conflict affiliation would take place between former opponents was affected by the context of the original aggressive incident. Insufficient individuals possessed all three types of conflict (food, social and no context) to allow simultaneous examination of conciliatory tendencies across the three categories at the individual level; Figure 3.2 therefore presents mean conciliatory tendencies simply using the maximum number of individuals which had eligible PC/MC pairs in each context. Pairwise comparisons were then conducted using those subsets of subjects which possessed data for at least two of the relevant context types. Individuals reconciled aggression over food (proportion of earlier pairs: 4/49; 1 later pair) significantly less frequently than incidents with no apparent context (63/309 EP and 9 LP; $CT_{none} = 0.19 \pm 0.05$, $CT_{food} = 0.03 \pm 0.05$; Wilcoxon: $N = 35$, $Z = -2.48$, $p = 0.013$). There was some indication that conflicts over social partners (proportion of EP: 12/41; 0 LP) were reconciled more

frequently than those over physical resources ($CT_{food} = 0.00 \pm 0.11$, $CT_{social} = 0.28 \pm 0.12$; Wilcoxon: $N = 13$, $Z = -1.83$, $p = 0.068$, NS). Finally, conflicts over social partners did not differ significantly in terms of conciliatory tendency from those with no obvious context ($CT_{social} = 0.31 \pm 0.08$, $CT_{none} = 0.19 \pm 0.06$; Wilcoxon: $N = 31$, $Z = -1.19$, $p = 0.235$, NS). Due to the small sample of social or food conflicts per individual, it was not possible to check the latter nonsignificant results by restricting analyses to subjects with more accurate scores (i.e. those with ≥2 eligible PC/MC pairs in both categories). However it seems likely that conflicts over social partners are reconciled at rates more similar to those following conflicts with no obvious context, than those following aggression over food.

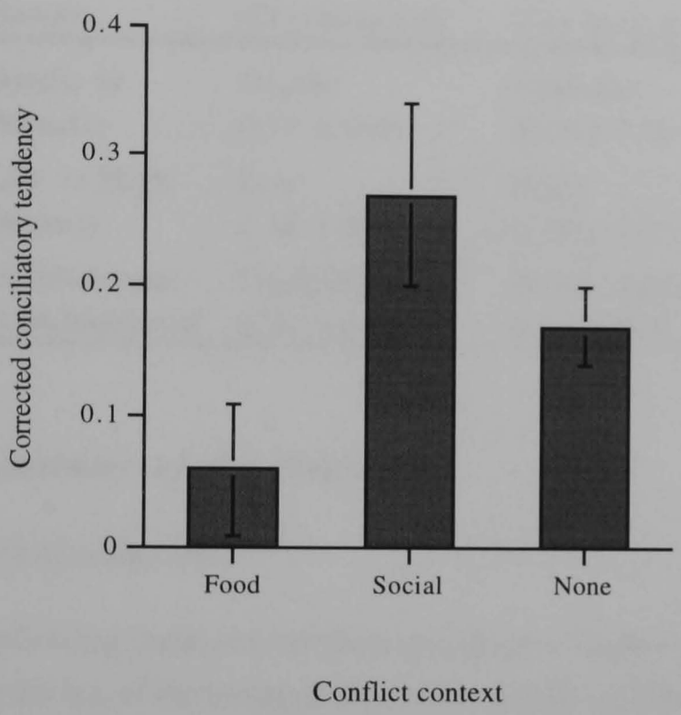



*Figure 3.2.* Mean (± SE) individual conciliatory tendency following conflicts occurring in 3 different contexts. Figures refer to the number of subjects contributing data toward each category.

*Other conflict characteristics*

Other salient features of the original aggressive incident did not significantly affect the likelihood that former opponents would engage in post-conflict affiliation. The results of the following analyses are presented in Table 3.1; all comparisons refer to Wilcoxon signed-ranks tests conducted upon individual CT scores. There was no significant difference between dyadic (20.9% EP and 2.2% LP, of 273 PC/MC pairs) and polyadic (17.8% EP and 3.1% LP, of 163 pairs) conflicts with respect to subsequent affiliative tendency between opponents. Conciliatory tendency did not differ significantly between low-intensity (threats through to lunges in the hierarchy of aggressive acts presented in Appendix B; 21.9% EP and 3.1% LP of 160 PC/MC pairs) and high-intensity (those

involving chases, manual contact, bites, or bidirectional aggression; 18.5% EP and 2.2% LP of 276 pairs) encounters. Nor did the directionality of aggression affect the tendency of former combatants to affiliate with one another; the proportion of earlier pairs following unidirectional conflicts (21.1%, versus 3.1% LP of 318 PC/MC pairs) was not significantly different from that following bidirectional conflicts (16.1%, versus 0.01% LP of 118 pairs). In all the above tests, comparisons remained nonsignificant when restricted to individuals possessing more accurate scores (i.e. two or more PC/MC pairs in each of the two categories being considered).

*Table 3.1.* Within-individual comparisons of corrected conciliatory tendency between former opponents following specific types of conflict.

| Feature | $CT_1$: Mean ± SE | $CT_2$: Mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|
| Dyadic vs Polyadic | Dyadic: 0.22 ± 0.04 | Polyadic: 0.14 ± 0.04 | 68 | -1.52 | 0.129, NS |
| Low vs High Intensity | Low: 0.18 ± 0.05 | High: 0.14 ± 0.03 | 65 | -0.65 | 0.515, NS |
| Unidirectional vs Bidirectional | Unidirectional: 0.20 ± 0.05 | Bidirectional: 0.14 ± 0.04 | 64 | -0.80 | 0.422, NS |

### *Attributes of the contestants*

#### *Sex of contestants*

Following same-sex conflicts conciliatory tendency did not differ significantly according to the sex of the initial protagonists. A post-conflict increase in affiliation between former opponents could be demonstrated following both conflicts between males (28.32% EP and 0.01% LP, from a total of 113 PC/MC pairs; Wilcoxon: $N = 46$, $Z = -4.14$, $p = 0.000$) and those between females (18.59% EP and 2.56% LP, of 156 pairs; Wilcoxon: $N = 52$, $Z = -3.46$, $p = 0.001$), and there was no significant difference in affiliative tendency between these two types of participant ($CT_{male} = 0.27 \pm 0.05$, $CT_{fem} = 0.16 \pm 0.04$; Mann-Whitney: $m = 46$, $n = 52$, $Z_{corr} = -1.54$, $p = 0.124$, NS). Restricting this analysis to those subjects possessing at least 2 eligible PC/MC pairs did not alter this outcome. Thus reconciliation appears to be a feature of the post-conflict period in both sexes.

However, conflicts between individuals of the same sex were more likely to be followed by affiliation than were cross-sex conflicts ($CT_{same} = 0.22 \pm 0.04$, $CT_{cross} = 0.09 \pm 0.03$; Wilcoxon: $N = 72$, $Z = -2.61$, $p = 0.009$). This result appeared to be due to the immature male subjects, within which this result could be demonstrated ($CT_{same} = 0.27 \pm 0.05$, $CT_{cross} = 0.06 \pm 0.04$; Wilcoxon: $N = 41$, $Z = -2.62$, $p = 0.009$), whereas

female subjects did not exhibit any significant difference in conciliatory tendency following intra-sexual versus inter-sexual aggressive encounters ($CT_{same} = 0.16 \pm 0.05$, $CT_{cross} = 0.12 \pm 0.05$; Wilcoxon: $N = 31$, $Z = -0.76$, $p = 0.445$, NS). Again, restricting the latter test to the female subjects possessing more accurate scores would not have altered this result.

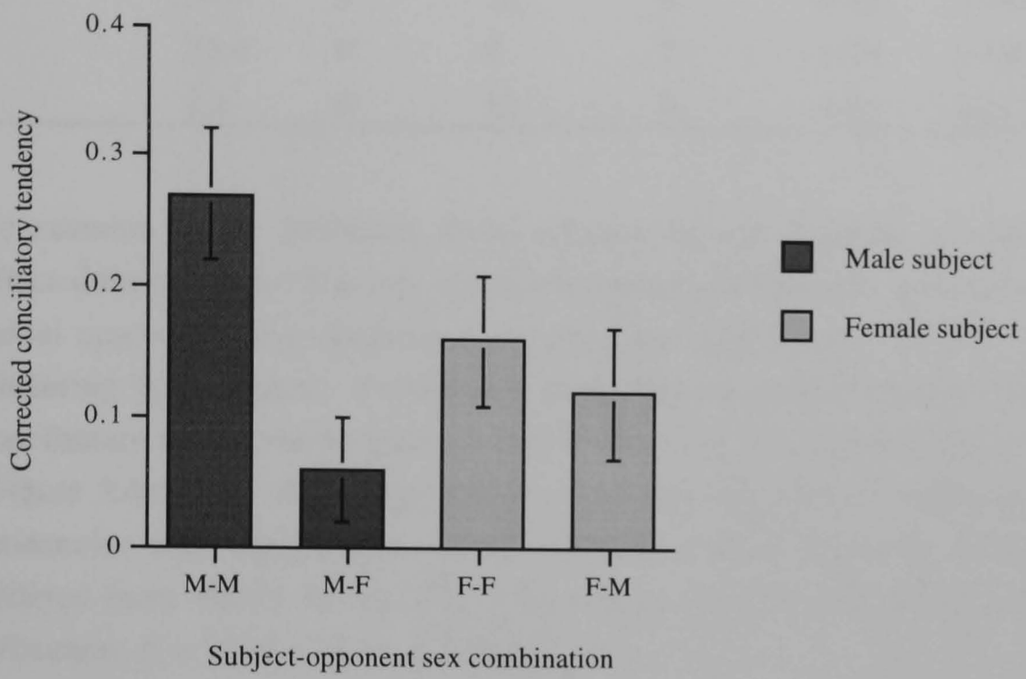



*Figure 3.3.* Mean (± SE) individual conciliatory tendency, according to sex of both the subject and its opponent. $N = 41$ male and 31 female subjects, respectively.

*Age of contestants*

Analyses of the effects of subject age upon reconciliation frequencies were limited by the fact that there were only 70 eligible PC/MC pairs in which the original conflict had been between age peers. Nevertheless, a significant post-conflict increase could be demonstrated within both the yearling and 2-year-old cohorts, but not within 3- and 4-year-old peers (Table 3.2); there was also a significant negative correlation between subject age and the corrected conciliatory tendency between age peers (Spearman: $N = 46$, $r = -0.35$, $p = 0.017$). These results should not be taken as an indication that older immatures do not reconcile at all, given the limitations of this dataset - small samples of individuals in the older age categories and very little data per individual (only 1 or 2 PC/MC pairs each), and given that previous studies on rhesus immatures of this age (e.g. de Waal & Johanowicz 1993, Judge *et al.* 1997) have demonstrated operationally defined reconciliation. However, it is possible that there could be a genuine difference in the importance of reconciliation *with peers*, according to subject age. More importantly, the

amount of data available for peers in the youngest age cohort (yearlings) seems sufficient to accept the positive result obtained as genuine.

*Table 3.2.* PC-MC comparisons for conflicts between peers, by age cohort.

| Cohort / yr | % EP | % LP | Total pairs | *N* | *Z* | *p* | |
|---|---|---|---|---|---|---|---|
| 1 | 44.1 | 0 | 34 | 23 | -3.18 | 0.002 | |
| 2 | 37.5 | 0 | 16 | 8 | -2.02 | 0.043 | |
| 3 | 25.0 | 0 | 8 | 7 | -1.34 | 0.180 | NS |
| 4 | 8.3 | 0 | 12 | 8 | -1.00 | 0.317 | NS |

To examine (at the individual level) whether the age disparity between adversaries affected the likelihood that they would subsequently affiliate, the age difference between initial opponents was categorised as either low (difference of 0 or 1 year) or high (differing by ≥2 years). Preliminary inspection of pooled data revealed that mean conciliatory tendencies declined sharply if opponents were separated in age by ≥2 years (Figure 3.4a). For individuals which possessed both types of opponent, conciliatory tendencies were significantly lower following conflicts between contestants which differed more widely in age (Fig. 3.4b; $CT_{low} = 0.29 \pm 0.05$, $CT_{high} = 0.04 \pm 0.03$; Wilcoxon: $N = 75$, $Z = -4.34$, $p = 0.000$).

### *Aspects of the focal-opponent relationship*

#### *Kinship*

As kinship was expected to affect the social interactions of female macaques more than those of males, this analysis was performed separately for male and female subjects. It might have been preferable to utilise only conflicts in which both contestants had been male - or both female - but as relatively few subjects possessed eligible conflicts with both close kin and less closely related opponents of the same sex, comparisons were simply performed separately for male and female subjects.

Whilst in male subjects there was no significant difference in conciliatory tendency with close kin as opposed to less related opponents (Fig. 3.5; $CT_{kin} = 0.14 \pm 0.08$, $CT_{other} = 0.16 \pm 0.05$; Wilcoxon: $N = 33$, $Z = -0.03$, $p = 0.972$, NS), a nonsignificant trend toward greater conciliatory tendencies with kin opponents could be discerned in female subjects ($CT_{kin} = 0.26 \pm 0.09$, $CT_{other} = 0.09 \pm 0.05$; Wilcoxon: $N = 30$, $Z = -1.83$, $p = 0.067$, NS). Checking these results using the more accurate scores of individuals possessing two or more eligible PC/MC pairs with each category of opponent confirmed that male immatures exhibited no significant difference in conciliatory tendency according

to opponent relatedness, but revealed a significant difference in immature females ($CT_{kin}$ = 0.32 ± 0.07, $CT_{other}$ = 0.01 ± 0.04; Wilcoxon: $N$ = 13, $Z$ = -2.53, $p$ = 0.011).

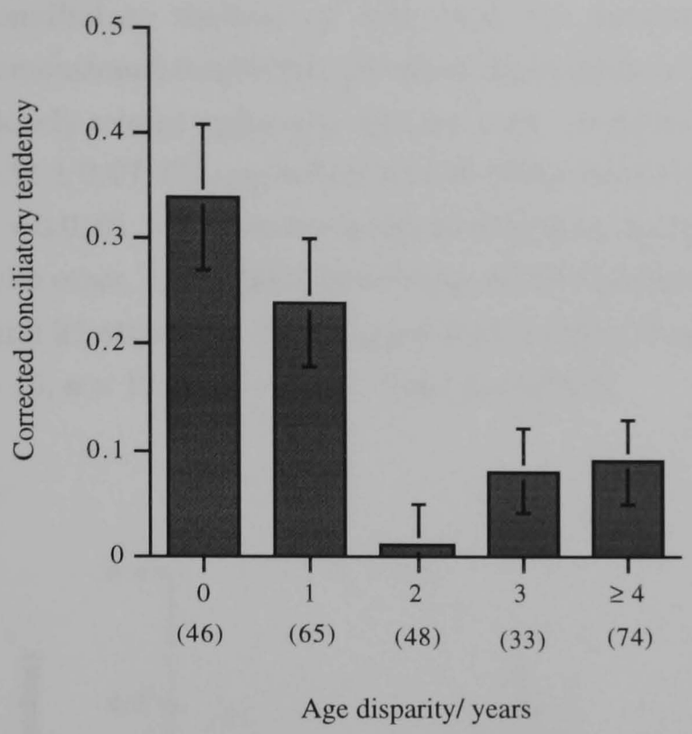



*Figure 3.4a.* Mean (± SE) individual conciliatory tendency according to age disparity between the opponents. Figures refer to the number of individuals contributing data in each category.


*Figure 3.4b.* Mean (± SE) individual conciliatory tendency following conflicts with opponents of low versus high age disparity. $N$ = 75 individuals.

Therefore the degree of kinship between former adversaries did not influence the level of post-conflict affiliation shown by or toward male subjects, whilst a kin-other distinction did seem to occur in conflicts involving female subjects. Indeed, a direct comparison of conciliatory tendencies with close kin between these male and female subjects demonstrated that female immatures had significantly greater conciliatory tendencies with closely related opponents than did males (individuals with ≥2 eligible pairs: $CT_{female}$ = 0.32 ± 0.07, $CT_{male}$ = 0.04 ± 0.08; Mann-Whitney: $m = 13$, $n = 13$, $Z_{corr} = -2.52$, *exact* $p = 0.019$), whilst male immatures exhibited significantly greater conciliatory tendencies with other, less related, adversaries when compared with female immatures (individuals with ≥2 eligible pairs: $CT_{male} = 0.15 \pm 0.05$, $CT_{female} = 0.01 \pm 0.04$; Mann-Whitney: $m = 13$, $n = 13$, $Z_{corr} = -2.05$, *exact* $p = 0.040$).

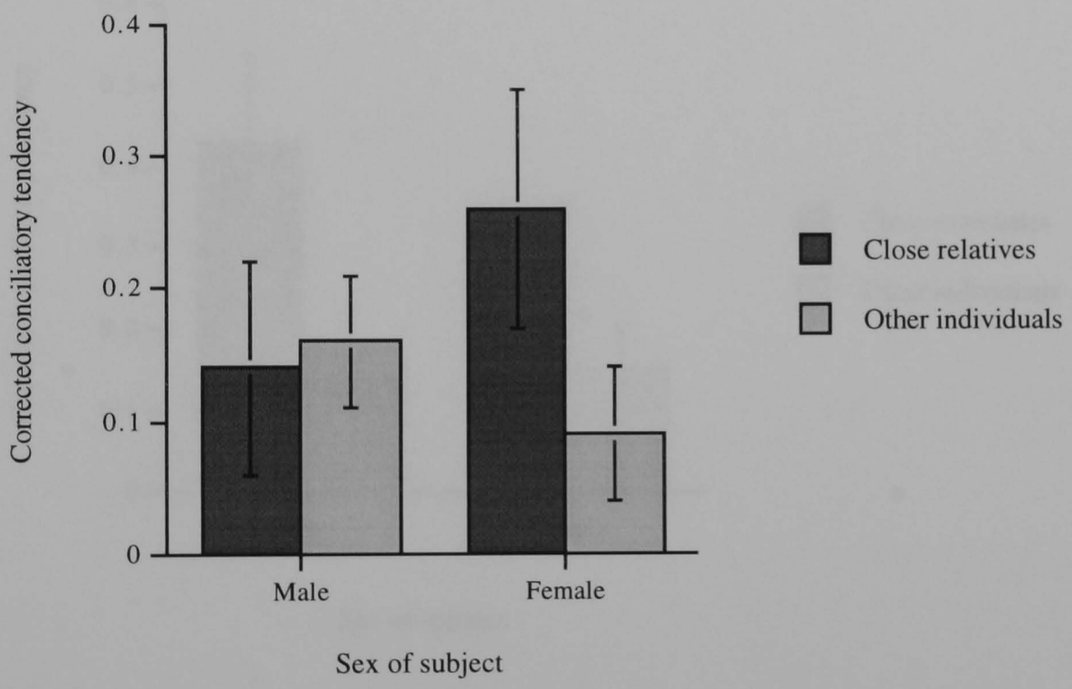



*Figure 3.5.* Mean (± SE) individual conciliatory tendency with closely related versus other opponents. $N = 33$ male and 30 female subjects, respectively.

*Frequent affiliates*

Finally, individual conciliatory tendencies were significantly higher following aggression between individuals which were close associates - defined as dyads in which at least one member fell within the upper quartile of the other party's contact affiliation scores - than after confrontations between less frequent affiliates ($CT_{close} = 0.40 \pm 0.07$, $CT_{other}$ = 0.16 ± 0.04; Wilcoxon: $N = 55$, $Z = -2.79$, $p = 0.005$). For the purposes of comparison with the results above concerning the effects of kinship, this test was also performed

separately upon male and female subjects. In both sexes, the tendency to reconcile was higher between close associates than between other opponents (Fig. 3.6; males: $CT_{close}$ = 0.43 ± 0.11, $CT_{other}$ = 0.17 ± 0.06; Wilcoxon: $N = 26$, $Z = -1.98$, $p = 0.048$; females: $CT_{close}$ = 0.36 ± 0.10, $CT_{other}$ = 0.15 ± 0.05; Wilcoxon: $N = 29$, $Z = -1.96$, $p = 0.050$). These results suggest that there may be a difference between male and female immatures in the degree to which their close associates also happen to be their maternal kin. In fact, the proportion of each individual's close associates which were close relatives was significantly greater in female immatures than in male immatures (group members between the ages of 1-4 years; females = 0.82 ± 0.02, males = 0.67 ± 0.04; Mann-Whitney: $m = 59$, $n = 57$, $Z_{corr} = -2.79$, $p = 0.005$).


*Figure 3.6.* Mean (± SE) individual conciliatory tendency following conflicts with close versus less frequent associates. $N = 26$ male and 29 female subjects, respectively.

### *Post-conflict affiliation with own supporters*

In 97 of the 165 polyadic conflicts, the focal subject received agonistic support from one or more other individuals. Focal immatures were more likely to affiliate with these supporters in the minutes immediately following conflicts than in control periods, the proportion of earlier pairs being significantly greater than that of later pairs at the individual level (41.5% EP versus 2.1% LP of 94 eligible pairs; Wilcoxon: $N = 60$, $Z = -4.70$, $p = 0.000$). Mean corrected affiliative tendency (AT) was relatively high, at 0.43 ($N = 60$ individuals), and 85.0% of the 40 first interactions observed in eligible PCs involved actual body contact. Supporters in these conflicts were typically close kin of the

beneficiary (63/94 = 67.0% of cases), or if unrelated were often close associates of the subject (defined on the basis of the group scan data; 10/31 = 32.3% of the remaining cases).

The relative cumulative frequency distributions of first affiliative acts in PCs and in MCs differed significantly (Fig. 3.7; Kolmogorov-Smirnov: $m = 40$, $n = 7$, $X^2 = 6.13$, $df = 2$, $p < 0.05$, 1-tailed), the maximal difference between the two distributions being located at <60 seconds. This time window was confirmed at the individual level, as focal subjects interacted affinitively with a former coalition partner within <60 seconds in a greater proportion of their PCs than of their MCs (PC = 0.314 ± 0.056, MC = 0.004 ± 0.004; Wilcoxon: $N = 60$, $Z = -4.20$, $p = 0.000$).

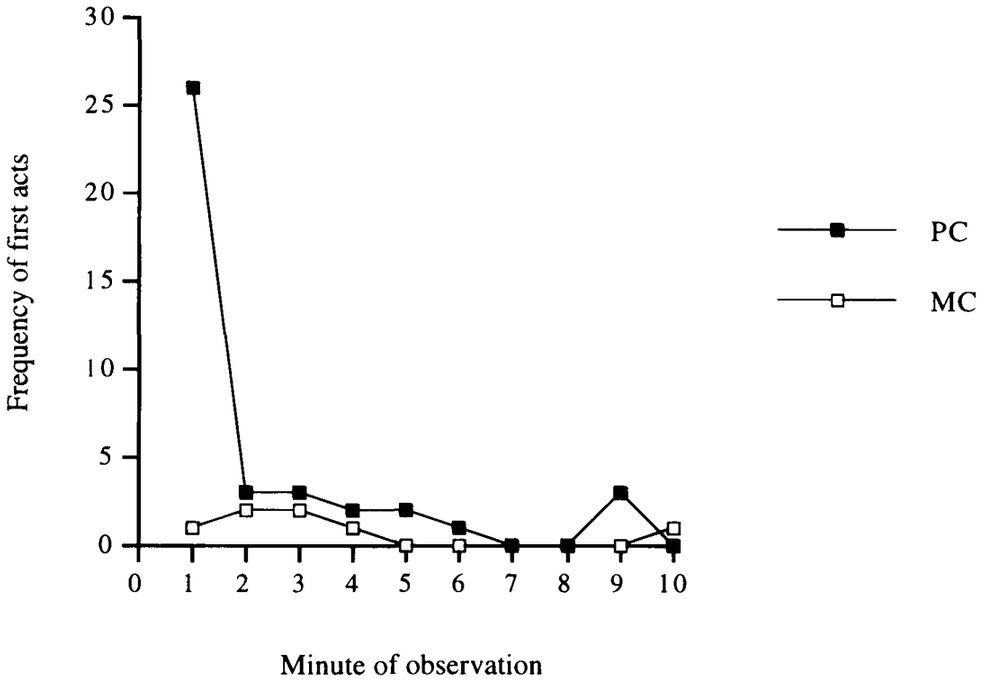



*Figure 3.7.* Distribution over time of first affiliative interactions with own supporters in aggregate post-conflict (PC) versus matched-control (MC) observations. From 94 PC/MC pairs.

*Selective attraction*

In order to check whether interactions involving former supporters were disproportionately increased in the aftermath of conflicts, corrected affiliative tendencies toward supporters (supp) were compared with those toward the "comparison group" of nonkin bystanders (non). The post-conflict increase seen with respect to coalition partners was significantly greater, demonstrating that the post-conflict attraction observed between immature subjects and their former supporters was selective ($AT_{supp} = 0.431 \pm 0.061$, $AT_{non} = 0.072 \pm 0.040$; Wilcoxon: $N = 60$, $Z = -3.82$, $p = 0.000$).

*Type of support provided*

Among the 94 eligible PC/MC pairs (provided by 60 different subjects), in 52 instances the conflicts had involved support of the aggressor, while the remaining 42 conflicts involved cases of victim support. There were too few individuals possessing conflicts of both types for a comparison at the individual level of whether post-conflict affiliative tendencies were affected by whether the partners had been aggressing together versus defending a victim in the previous conflict. However, 46.2% of the aggressor-support conflicts were followed by affiliation between the coalition partners at some point within the subsequent 10 minutes, and 38.1% of the victim-support conflicts. If this assessment was restricted to PCs in which the first act of affiliation between former supporters occurred within the initial <60 second window, the figures were 30.2% and 25.0% respectively. Therefore there was no real indication that the type of intervention involved appreciably influenced whether or not the donor and beneficiary of support subsequently interacted affiliatively.

*Initiative to affiliate*

Ideally, one would compare the proportion of instances in which the donor (versus the recipient) of support had taken the initiative to affiliate in PC and MC observations, at the individual level. With only 7 first affiliative acts between subjects and their supporters being recorded in the MCs, such an approach was clearly not feasible. However, a descriptive analysis strongly suggested that the recipient of support was usually responsible for post-conflict affiliation. In 83.8% of the 37 first acts which took place in eligible PCs (3 PCs containing affilition between former coalition partners, but which followed conflicts in which the two individuals had simultaneously aggressed against their common target, had to be excluded because donor and recipient could not be distinguished), it was the beneficiary of support which initiated the interaction. Restricting this comparison to only the 25 first events which fell within the initial <60 seconds of eligible PCs produced similar results (84.0% initiated by the beneficiary of support). Nor did the outcome seem to differ depending upon the type of aid donated, as in 81.0% of 21 instances following aggressor-support it was the recipient which took the initiative, compared with 87.5% of the 16 first events following victim-support.

## *Discussion*

*The occurrence of, and initiative to, reconciliation*

Operationally defined conciliatory behaviour was found to occur in immature members of two groups of free-ranging rhesus macaques. Former opponents interacted affiliatively sooner and more often following aggressive disputes than under baseline conditions, with first bouts typically taking place within 200 seconds of conflict termination. These friendly reunions were selective, in that the magnitude of the post-conflict increase in affiliation with previous opponents was significantly larger than the equivalent increase with a comparison category of other group members (the latter defined as unrelated third parties, a definition which will be retained throughout this thesis). Furthermore, the post-conflict increase held even after statistically controlling for inter-opponent distance at the beginning of observations, and hence cannot be ascribed to differential proximity under the two conditions (see Call 1999, Call *et al.* 1999, for further discussion of how failure to take this factor into consideration may compromise analyses). These results therefore concur with and extend previous studies of captive populations, which show that juveniles of several simian species engage in reconciliatory interactions by the age of two years or earlier (rhesus macaques: de Waal & Johanowicz 1993, Judge *et al.* 1997; longtailed macaques: Cords & Aureli 1993; brown capuchins: Weaver & de Waal, in press). In this study, conciliatory behaviour was apparent even in the youngest age cohort studied - yearlings - with conflicts between peers of this age actually being reconciled more often than those between older agemates. Whilst this outcome might simply reflect the changing importance and accessibility of peers as partners at different ages, it nevertheless demonstrates that operationally defined reconciliation does occur even when both participants are only one year old. This is in line with the view that cercopithecines may be under pressure to acquire conflict management skills at a relatively early age; the special period of tolerance by their elders which marks early infancy often ends well before weaning (Berman 1980, Altmann 1980, Horrocks & Hunte 1983), and from thereon youngsters are disproportionately frequently the targets of conspecific aggression (e.g. Dittus 1977, Silk *et al.* 1981, Pereira 1988b). Additionally, the process of rank acquisition over older but "lower born" groupmates (Datta 1983a) commences early, with both infants and juveniles increasingly instigating or joining in aggression in attempts to better their own dominance position (Bernstein & Ehardt 1985c, Prud'homme & Chapais 1996). Thus the use of behaviour patterns such as reconciliation, which can mitigate the negative consequences of involvement in aggression (see introduction for details), is likely to be a necessity even in very young juveniles.

Rhesus macaques exhibit conciliatory tendencies at the lower extreme of those measured in primates (for possible reasons and comparison with other species, see Thierry, in press). Recalculation of conciliatory tendencies documented in earlier studies of captive rhesus (de Waal & Yoshihara 1983, de Waal & Luttrell 1989) using a measure which fully corrects for baseline levels of affiliation (Veenema *et al.* 1994), together with reconciliation rates derived in more recent studies of this species, reveal corrected values of 10% or under in mixed-age samples (Call *et al.* 1996, Thierry, in press). Mean individual corrected conciliatory tendency in this sample of immatures was 18%, a relatively high figure, although still very much at the lower extreme for macaques. It is possible that the fact that at least one of the combatants was an immature in this study is responsible for the apparently elevated rates of reconciliation, as in several species conflicts between immatures are reported to be reconciled at greater rates than those between adults (e.g. Thierry 1986, Schino *et al.* 1998). Why this should be so is not known at present. However, it is also possible that methodological differences could in part account for the higher conciliatory tendencies observed in this study. Since all overt attempts at post-conflict reunion were of interest, even interactions between former opponents consisting solely of vocalizations and/or unreciprocated overtures were included in analyses. If such unilateral acts are *particularly* likely to occur under post-conflict conditions (for example because recent victims may be wary of approaching their former adversaries too closely), then previous studies of rhesus macaques which adopted a strict definition of reconciliation emphasizing interactions involving actual body contact (e.g. de Waal & Yoshihara 1983, Call *et al.* 1996) potentially scored only a subset of the conciliatory actions which may have taken place, and this reduction may have applied disproportionately to PC (as opposed to MC) interaction levels. In this study, adoption of a very strict criterion for reconciliation (scoring only bouts involving prolonged contact and/or bidirectional affiliative signals) did indeed result in a slightly lower mean conciliatory tendency (14%). However, given that a number of studies have suggested that affiliative signals directed toward a former opponent whilst in proximity are *disproportionately* increased in comparison to other forms of interaction (such as physical contact) in the aftermath of conflicts (e.g. Silk *et al.* 1996, Verbeek & de Waal 1997), and that even unilateral affiliative gestures have been demonstrated to influence the behaviour of former adversaries in a positive fashion (at least when performed by the former aggressor: Cheney & Seyfarth 1997; see also Cords 1993), adoption of more inclusive criteria for reconciliation would seem preferable.

There was a slight tendency for former victims to initiate post-conflict rapprochement, although no formal test of this issue was performed. Theoretical considerations suggest that in macaque taxa with relatively strict dominance styles (de Waal 1989a), in which the initiator and victor of an aggressive encounter is typically the dominant party and recipients of aggression rarely retaliate either during or following the initial confrontation

(see also chapter 4), former victims should have the most to gain if reconciliation takes place. This is because it is the victim which is most at risk of receiving further aggression in the immediate future and would therefore benefit from increasing the predictability of its former adversary's actions, and because in the long-term a dominant individual may have more to offer in the way of benefits (e.g. in permitting access to resources, or effective agonistic support) and be more costly to have as an enemy, than would a subordinate individual. Balanced against this, however, is the fact that the risk of further aggression may make victims reluctant to approach their former attackers in order to reconcile (de Waal & Ren 1988), unless the latter has already given some indication that it would be receptive to such an overture. Even then it is important to accurately assess an opponent's motivation, as on occasion former aggressors give affiliative signals only to instantly resume aggression once their target comes within reach (reported in Cheney & Seyfarth 1990a and de Waal 1986d). Such sequences were observed in at least 2 of the 63 post-conflict observations in which the first bout of affiliation between opponents took place within 200 seconds; both cases involved juvenile brothers, the duped victim being the younger sibling. These risks might explain why a high proportion of initial reunions between opponents were characterised by signals such as vocalizations - only 59% involved body contact between the contestants within the first bout of affiliation, and in a proportion of these a vocalization or facial signal in any case preceded the contact - perhaps because victims were wary of approaching without first "testing the water" and/or might be likely to respond to the aggressor's approaches or signals with avoidance behaviour. In contrast, first bouts of affiliation which took place between former coalition partners or between a contestant and its own kin in the aftermath of conflicts (situations where there should be little risk of animosity between the individuals concerned) were much more likely to achieve physical contact within the initial bout, at 85% and 88% respectively (data on affiliation with related bystanders being drawn from chapter 5).

Thus the patterns of initiation actually observed may reflect only the outcome of weighing these opposing factors, the relative strength of which should determine whether aggressors or victims are more likely to take the responsibility for initiating reunions. This might explain the inconsistent results obtained in previous studies of relatively despotic species; in some aggressors instigate reconciliation most often (e.g. rhesus macaques: de Waal & Yoshihara 1983, de Waal & Ren 1988; longtailed macaques: Cords 1988) whilst in others the victim has instead been proposed (longtailed macaques: Aureli *et al.* 1989; pigtail macaques: Judge 1991). On the other hand, some of the disparity in results may be due to differences in methodology between studies, for example in whether only those reunions which took place within a predefined early time "window" were utilised or whether all first interactions which occurred at any point in post-conflict observations were examined - Aureli *et al.* (1989) have shown that patterns of initiative

may change over time in PCs, with those recorded later on reverting to the pattern characteristic of baseline conditions. Secondly, where unilateral affiliative gestures have not been scored as "reconciliations" it is possible that not only are many overt initiatives overlooked, but also that those more likely to be made by a particular type of contestant (e.g. aggressors or victims) are specifically under-represented. Finally, it may be difficult or impossible to accurately gauge conciliatory motivation, given that subtle shifts in posture or glances by one or other party may be the initial signal of willingness to interact yet go unrecorded, and because even a highly motivated individual may not attempt a reunion if it perceives that such an overture is likely to be unsuccessful (Cords & Aureli, in press). Our current methods of examining initiative may be poor measurements therefore.

*Attributes of the conflict*

The nature of the aggression constituting a conflict did not appear to affect the likelihood of reconciliation - neither the number of participants, the severity of the aggression used, nor its directionality were associated with significant variation in conciliatory tendency. Inconsistent results have been obtained in previous studies which examined these factors. Most studies found no difference in conciliatory tendency between dyadic and polyadic conflicts, whilst more intense conflicts have been reported to either increase (de Waal 1987), decrease (Schino *et al.* 1998) or, most often, to have no significant effect upon levels of reconciliation (Cords & Aureli 1993, Abegg *et al.* 1996, Castles & Whiten 1998a, Call *et al.* 1999), in different species. The degree to which dominance asymmetries are weak and aggression often bidirectional is one - of several - characters which covary with conciliatory tendency in interspecific comparisons, with species in which counteraggression is relatively frequent tending to have higher rates of reconciliation (Thierry 1986, in press, de Waal & Luttrell 1989, Ren *et al.* 1991, Petit & Thierry 1994b). This result has been interpreted as stemming from a greater need in both parties to reduce uncertainty concerning an adversary's future actions (Aureli *et al.* 1989) or to signal their own benign intent (Silk 1996), in cases where the recipient of aggression is likely to retaliate rather than acquiesce. However, in only a few of the studies which compared bidirectional and/or undecided conflicts versus unidirectional altercations with a clearcut outcome within the same species have the former been associated with a greater likelihood of reconciliation (e.g. Aureli *et al.* 1989, Kappeler 1993; but see Cords & Aureli 1993, Petit & Thierry 1994c, Castles & Whiten 1998a, Schino *et al.* 1998 for contrary results). It seems fair to say that, by and large, features of the aggression *per se* are not a major contributor to any variation in conciliatory tendency seen within groups.

In contrast, one aspect which has been consistently associated with differences in the likelihood of reconciliation is the context of a conflict. In a variety of species, disputes over food are either reconciled at substantially lower rates than those with no obvious cause (Aureli 1992, Castles & Whiten 1998a; see also Matsumura 1996), or no evidence for reconciliation has been found at all (de Waal 1984, Koyama 1997, Verbeek & de Waal 1997). In the present study, aggression in a feeding context was associated with significantly reduced conciliatory tendencies. One possibility is that reunions occur at low rates following conflicts over food because one, or both, participants are preoccupied with consumption of the disputed resource, and rapprochement is simply postponed until they have finished eating. However, in an earlier experimental study on juvenile rhesus macaques the food (pieces of apple) which had provoked aggression was invariably consumed within the first 10 minutes of the post-conflict period, yet there was no indication of reconciliation taking place in the remaining portion of the 30-minute observations (de Waal 1984). Similarly, in Koyama's (1997) study of Japanese macaques no evidence for delayed reconciliation following confrontations which took place at feeding time was found, even when post-conflict observations were extended for up to 90 minutes. Thus the frequency of reconciliation genuinely seems to be lower following contest competition over edible resources.

A proximate explanation of this difference is provided by the finding that rates of self-scratching - thought to be a reflection of the uncertainty and anxiety that aggression may induce, a factor which may motivate reconciliation attempts (Maestripieri *et al.* 1992, Aureli 1997) - were significantly lower following conflicts in a feeding context (see chapter 4 for further details). This result was not due to systematic differences in either the intensity of the original conflict or the overall risk of receiving subsequent attacks, and it is therefore suggested that the greater predictability of aggression occurring in the presence of food occasions less stress in the participants and hence lowers their motivation to reconcile. In ultimate terms, it has been suggested that conflicts over access to essential resources may somehow be less damaging to relationships than are other types of conflict (Aureli 1992). That is, the consequences may be limited to loss of the resource, without necessarily altering the nature or patterning of subsequent interactions between the parties concerned. Perhaps some support for this suggestion is provided by Koyama's (1997) finding that while grooming rates between former opponents in the 10 days following unreconciled conflicts were significantly lower than baseline rates in the overall sample, in cases where the aggression had concerned food there was no significant difference between post-conflict and baseline grooming rates for the dyad in question. However, as this result was based upon only 17 conflicts occurring at feeding time, further investigation of this issue would be useful. On the other hand, it is possible that aggression concerning food does endanger the relationship between contestants, but that the benefits of consuming the disputed resource (which has an immediate and direct

effect upon fitness) outweigh the decrement a relationship may incur due to a failure to reconcile any one incident, as multiple insults to a relationship may be endured before its demise and because maintenance of relationships has only an indirect future effect upon fitness (Das 1998).

The results concerning rates of reconciliation following conflicts over access to social partners are more difficult to interpret. There was some indication that such confrontations produced relatively high conciliatory tendencies, although further data are required in order to confirm whether the (nonsignificant) increase discerned holds. In proximate terms, one might have expected such encounters to be relatively predictable and thus to have been associated with low conciliatory tendencies; being in the vicinity of or interacting with particular individuals can be a situation likely to provoke attacks by higher-ranking associates (which may themselves wish to interact with the partner in question) or relatives of the latter (for example where the partner is a young infant), and individuals may learn through experience to expect aggression when in such situations. However, the greater variability of the concilatory tendency values associated with this context may well reflect the fact that the conflicts assigned to this category were relatively heterogeneous - only some were clearly disputes over access to a partner, whereas others arose, for example, when an infant's squeal prompted a neighbouring individual to attack an innocent passerby. Thus not all conflicts counted as "social" were necessarily particularly predictable. Unfortunately, the low number of conflicts of this type precluded more detailed analysis at the individual level, and thus it was not possible to investigate how levels of self-scratching by contestants following conflicts over social partners compared with those in other contexts. Alternatively, contestants (particularly those which lost) may in fact be highly motivated to reconcile such conflicts, as a means of regaining or maintaining access to the disputed partner rather than through any desire to interact with the former opponent itself. This interpretation would predict relatively high conciliatory tendencies, and echoes previous findings that conflicts between adult female baboons were reconciled at relatively high rates when at least one of the protagonists possessed a dependent infant (Castles & Whiten 1998a, Silk *et al.* 1996) - attraction to the infants may have prompted the post-conflict interactions with their mothers.

*Attributes of the protagonists*

The age and sex combination of former adversaries was associated with marked variation in their tendency to affiliate in the wake of aggressive confrontations. Operationally defined reconciliation could be demonstrated in both sexes of immature. In adult rhesus, males have been distinguished as the more conciliatory sex (de Waal 1984), with females exhibiting lower conciliatory tendencies or at least being more selective in the choice of

partners offered reconciliation (de Waal 1986b). However juvenile females were described as being more similar to male peers in this respect (de Waal 1984), which is consistent with the absence in this study of any significant difference between male and female subjects in reconciliation rates following within-sex conflicts. Aggression between opponents of the same sex was reconciled at much higher rates than that between the sexes, a pattern also documented in several other macaque taxa (e.g. Cords & Aureli 1993, Schino *et al.* 1998). The pattern of results obtained here suggested that male immatures were responsible for most of this difference, as male subjects were involved in friendly reunions significantly more often with same-sex as opposed to cross-sex opponents, whilst immature female subjects exhibited no such distinction. Under most circumstances, affiliative acts tend to be more biased toward same-sex partners in young males than in young females. Immature male macaques associate preferentially with male partners from an early age, and whilst any bonds with females are broken upon natal emigration, their early friendships with male groupmates may persist following joint immigration into other troops (for references and further details, see section on kinship below). In general, relationships with other males are therefore likely to be both more compatible (in terms of having a history of positive interaction, cf. Cords & Aureli 1993) and more valuable (in terms of their long-term potential) to immature males than those they have with females, and both factors are likely to produce higher rates of reconciliation in the former category of dyad. In contrast, female association patterns are largely governed by kinship, an attribute which cuts across age and sex categories, and thus the distinction between same- and cross-sex bonds may be less marked in young female subjects.

Opponents which differed in age by two or more years were significantly less likely to reconcile than those which were more closely matched in age. Some indication of a similar effect has also been found in work on juvenile rhesus (P. Judge, pers. comm.) and Japanese macaques (Schino *et al.* 1998) in captivity. In both these studies, conflicts between two immatures were reconciled significantly more frequently than those between an immature and an adult (with indications of a similar effect also being apparent in de Waal & Ren's 1988 study of stumptail macaques). Again, it seems likely that two factors, relationship value and partner compatibility (Cords & Aureli 1993), act in concert to produce such results. Firstly, reconciliation rates may be low between contestants which differ widely in age because their relationship is not particularly valuable to the older party, who is therefore unlikely to initiate a reunion. Due to their small size and on average low rank juveniles are usually not in a position to provide effective agonistic support or other benefits to older animals, especially in comparison with those available from other, more mature, partners who may therefore be rated more highly (cf. market effects, Noë & Hammerstein 1995). It is also worth considering the possibility that relationships with older, but unrelated, group members may possess less value than those

with peers from the immature contestant's point of view as well. A partner's value derives not only from the level of benefits it can provide but also from its availability and tendency to act in such a manner (Kummer 1978). In rhesus macaques, adult partners can provide the best protection and access to resources, but if unrelated to an immature they may be unlikely to do so. Peers, which have similar needs and may be willing to exhange the greatest range of benefits (cf. de Waal 1991a, Kapsalis & Berman 1996b) may thus be relatively valuable partners, at least for juvenile group members. Strong bonds between agemates may also be favoured via kin selection, given that biasing of affiliation and reconciliation toward peers may have the consequence of favouring paternal siblings, although such effects are more likely to occur where groups are small and/or male tenure is of relatively long duration (Altmann 1979).

A second, proximate, explanation for these results is that young subjects may be particularly reluctant to approach former opponents which are substantially larger and/or higher-ranking than themselves. In the Cayo Santiago rhesus, an age difference of two years typically corresponds to an approximate doubling of body weight and linear size measures (A.J.N. Kazem, unpublished data; see also Turnquist & Kessler 1989) relative to that of the younger party, at least when the latter is a juvenile or infant. Relative rank of immature individuals is also influenced by relative age, and hence size. Amongst prepubertal females lower-born but larger individuals can outrank prospectively dominant partners, particularly if the size disparity is large, whilst dominance relations between male immatures and partners of the same sex are primarily determined by relative age/size (A.J.N. Kazem, unpublished data, Kazem 1993; reviewed in Lee & Johnson 1992, Pereira 1992, 1995). In conflicts between animals of very disparate age the younger contestant is typically the victim, and under these conditions the compatibility of the partners involved may be an important constraint limiting the occurrence of reconciliation; the former victim may be unwilling to take the risk of approaching or initiating affiliation with such an opponent unless the dyad happens to have a history of nonaggressive social interaction in other contexts.

*Effects of the quality of relationship between opponents*

Individuals were more likely to reconcile with closely related opponents than with other group members, a result which has usually been interpreted as reflecting the differential value of these two types of partner. Partners which frequently support one another in coalitions and/or tolerate each other around resources are considered to be particularly valuable, and in many macaque taxa there is a pronounced kin bias in the donation of support, particularly where more costly forms - such as defending targets under attack - are concerned (e.g. Kurland 1977, Massey 1977, Bernstein & Ehardt 1985a, Kaplan *et al.* 1987). In rhesus and Japanese macaques the majority of interventions in favour of

juvenile group members are made by close relatives such as mothers, aunts and older siblings, and in young females such aid is a critical factor in the acquisition and maintenance of rank above lower-born families or individuals (Berman 1982, Datta 1988, 1992, Chapais 1988, 1992). Close relatives are also preferentially tolerated in competitive situations, for instance at monopolizable feeding or drinking sites (Yamada 1963, de Waal 1986c, 1993b, Kapsalis & Berman 1996b). Cooperation is most heavily biased toward the matrilineal network in these and other macaque species characterised as "despotic" (see chapter 2; Thierry 1990, in press), and it is in these taxa that a distinction between kin and nonkin in reconciliation frequency is most evident (Aureli *et al.* 1997; see also Veenema *et al.* 1994, Call *et al.* 1996).

However, the importance of kin bonds differs between the sexes. In many papionines, juvenile males receive less agonistic support from their adult female kin than do young females, and dominance relationships between young males are less dependent upon familial aid and social position than are those between females (e.g. Pereira 1989, 1995, Lee & Johnson 1992; A.J.N. Kazem, unpublished data). Even in the most nepotistic species, male immatures associate preferentially with same-sex peers, brothers, and older male troop members from an early age (Colvin 1983, Ehardt & Bernstein 1987, Nakamichi 1989, van Noordwijk *et al.* 1993). In contrast, weanling females rapidly become integrated into the matrilineal network, forming their closest associations with female relatives and generally preferring female associates, especially high-ranking ones (references above; see also Cheney 1978, Fairbanks & McGuire 1985, Glick *et al.* 1986). These differences are likely to reflect sex-specific life histories and consequent differences in the long-term benefits of investing in relationships with particular classes of individual. In taxa which exhibit female natal philopatry affiliative bonds formed between females, both kin and nonkin, can and do persist into adulthood (e.g. Fairbanks 1993a, O'Brien & Robinson 1993). Males become increasingly peripheral members of the group as they mature, and their bonds with female kin are broken upon emigration from the natal group at the time of puberty. However, in several cercopithecine species young emigrés often transfer with peers or siblings, or preferentially immigrate into neighbouring groups containing older males from their natal troop (e.g. Cheney & Seyfarth 1983, van Noordwijk & van Schaik 1985, Zhao 1996). In some cases these male associates are also known to continue to affiliate and support one another in their new group, which can improve their rank (Meikle & Vessey 1981), whilst the safety thereby provided may have important survival consequences (Rajpurohit & Sommer 1993). A similar sex difference was discerned in the current study - among female immatures a significantly greater proportion of each individual's close associates (defined on the basis of the distribution of contact affiliation scores with different partners in an independent dataset) were close maternal relatives, when compared with the preferred associates of immature males. Furthermore, a difference in conciliatory tendency toward

close kin versus less related opponents was exhibited only by female subjects. If maternal kin are less important to young males (and *vice versa*) than to females, and unrelated partners are relatively more important, this would explain the lack of such a result among the male subjects.

However, *both* male and female immatures displayed greater conciliatory tendencies following conflicts with individuals known to be close associates as compared to opponents which were less frequent affiliates (see also Cords & Aureli 1993, for a similar result in juvenile longtailed macaques). In combination with the sex-specific association between kinship and "friendship" described above, this suggests that bond strength *per se* is likely to be the more important factor in determining whether reconciliation occurs. That is to say, the effect of kinship upon conciliatory tendency in female subjects may have been due to the fact that maternal relatives have, on average, closer bonds in this sex, rather than being determined by the indirect fitness benefits to be gained from preferentially maintaining relationships with one's kin. Kinship and high affiliation are often confounded, and previous studies have differed in whether or not the two factors exert independent effects upon reconciliation frequencies (Veenema *et al.* 1994). For example, whilst de Waal & Yoshihara (1983) found that in rhesus macaques the effect of kinship upon conciliatory tendency disappeared if social bond strength (measured as contact time, as here) was taken into account, other studies have found that the kinship effect nevertheless persists (e.g. longtailed macaques: Aureli *et al.* 1989; Japanese macaques: Schino *et al.* 1998). Unsurprisingly, in the more egalitarian macaque taxa - in which kinship biases in affiliation tend to be less pronounced - friendship plays a more important role than kinship in determining reconciliation frequencies (e.g. stumptail macaques: de Waal & Ren 1988, Call *et al.* 1999). The fact that kinship, close affiliation, and indeed rank disparity tend to covary in macaques, at least in adult females, is one reason why the use of multivariate methods (cf Schino *et al.* 1998, Call *et al.* 1999) to simultaneously evaluate the contributions of these variables is to be preferred.

Finally, the effects of both bond strength and kinship upon conciliatory tendency have often been interpreted in terms of the greater benefits of maintaining relationships with partners presumed to be of high value. However, as Cords & Aureli (in press) have cautioned, neither kinship nor frequent affiliation (at least as defined in most studies, although see Aureli *et al.* 1989, Cords & Aureli 1993) are actually direct measures of partner *value*. The fact that in both cases it is individuals which also show high levels of affiliation under other circumstances (by definition, in the case of close associates) which reconcile at the greatest rates suggests that the greater *compatibility* of these dyads might equally account for the results obtained. By increasing the predictability of an opponent's reaction to any affiliative overture, greater compatibility potentially lowers the costs of reconciliation attempts, which therefore may be more likely to occur. In practice, partner

value and compatibility are likely to covary, and in observational studies it is difficult to distinguish between the two (Cords & Aureli 1993, Schino *et al.* 1998). Clearly the latter, proximate, explanation need not detract from an ultimate one based upon partner value, but it is worth pointing out that not all individuals classed as kin or close associates are necessarily highly valued partners. Other proximate factors may also play a part. For example, if particular types of dyad exhibit different tendencies to remain in proximity after the termination of conflicts, this in itself could create the observed variation in rates of reconciliation. Relative inter-opponent distance at the commencement of paired PC and MC observations can have a large influence upon estimates of conciliatory tendency (Call 1999), and in stumptail macaques unrelated opponents are known to disperse further after conflicts than do closely related adversaries (Call *et al.* 1999). The question remains why, for a given intensity of aggressive encounter, this should be so. As the authors point out, it is possible that individuals with a more conciliatory attitude are more likely to remain in the vicinity, with the distance adopted perhaps itself functioning as an indicator of their intent to reconcile. In this case, rather than short inter-opponent distances creating the enhanced reconciliation rates observed between relatives, the greater motivation of these individuals to reconcile (perhaps for the reasons given above) might be the cause of their lower degree of spatial separation.

*Affiliation between supporters following polyadic conflicts*

Affiliation between coalition partners was also more likely to occur under post-conflict than under baseline conditions, an increase which proved to be selective. It is possible that this post-conflict increase might have occurred simply because supporters were more likely to be in the vicinity of (and hence more "available" to) subjects immediately following conflicts than at other times, rather than constituting a real change in the motivation of these group members to interact. Unfortunately, as complete proximity data were not collected at the beginning of MC observations, it was not possible to check whether a significant post-conflict increase would have remained even after correcting for any disparity in inter-individual distance between coalition partners. Nevertheless, two observations suggest that the effect demonstrated was unlikely to have been an artefact. Firstly, former adversaries are also more likely to be in close proximity immediately following aggressive encounters, yet the degree of post-conflict increase in affiliation between these individuals was much lower than that observed between former coalition partners (mean corrected affiliation tendencies of 0.18 versus 0.43, respectively). Furthermore, in the majority of cases supporters were either close relatives or known close associates of the focal animal. These group members are particularly likely to be near one another under baseline conditions (by definition, in the latter case), which would diminish the chances of demonstrating that affiliation occurred significantly earlier following conflicts than at other times. However, this final point does raise the issue of

whether these post-conflict interactions took place predominantly because coalition partners tended to be maternal kin (or at least close associates), or specifically because of the support they had donated. After all, a post-conflict increase in affiliation was also demonstrated between immature contestants and those maternal relatives which had not participated in the aggressive event (see chapter 5).

Affinitive exchanges between the members of one faction in the aftermath of polyadic conflicts have previously been reported in mixed-age samples of captive rhesus macaques and wild olive baboons (de Waal & Yoshihara 1983, Castles & Whiten 1998a; although in the latter case no information on selectivity toward this partner class has been provided), but no selective increase was apparent in captive stumptail macaques (de Waal & Ren 1988), and the possible functions of such interactions have not yet been explored. Coalition partners might be motivated to affiliate for reasons similar to those which would apply to post-conflict interaction between contestants and familiar individuals in general (e.g. one's own relatives). For example, a high proportion of first bouts involved body contact, which might be sought by both the donor and beneficiary of support as a means of mutually reducing the arousal and/or distress which participation in confrontations can produce (see references in chapter 4). Grooming, at least, appears to have an intrinsically calming effect (Terry 1970, Goosen 1975) and its receipt has been shown to prompt a decline in physiological and behavioural indicators of sympathetic activation such as heart rate and self-scratching (Schino *et al.* 1988, Boccia *et al.* 1989, Aureli *et al.* 1999). Whether contact with former supporters (or indeed with one's relatives) can produce a more rapid decline in these indicators than would otherwise occur in the aftermath of aggression has yet to be tested. Such an effect upon rates of self-scratching has been demonstrated following reconciliation between opponents (Aureli & van Schaik 1991b, Castles & Whiten 1998b, Das *et al.* 1998), but not following post-conflict affiliation between aggressors and their former opponent's kin nor that with unrelated bystanders (Das *et al.* 1998).

Secondly, contestants might seek proximity and/or interaction with likely supporters in order to reduce the risk of receiving renewed attacks from their original adversary or opportunistic aggression from bystanders (see chapter 5 for further discussion of this point) - a strategy which should be particularly effective where the social partner concerned has recently demonstrated its willingness to actually provide agonistic support. This in itself might reduce anxiety and uncertainty on the part of the contestant about the future actions of others. Affinitive overtures between former coalition partners were invariably conspicuous, often involving excited vocalizations as one party mounted or clasped the other before settling into peaceful grooming. Therefore it is possible that such reunions might not only explicitly reaffirm the bond between a contestant and its partner, but could also signal their solidarity to nearby group members by drawing the fact that support has taken place to the attention of others. If these interactions can be

confirmed to possess distinctive behavioural characteristics their performance would bear resemblance to the specific threat calls given by Japanese macaques when engaging in aggressor support, vocalizations which have been proposed to function in advertising the caller's provision of support for particular high-ranking individuals more widely (Machida 1990). Nevertheless, even grooming can act as a marker of the bond between two individuals, and there is evidence that macaques do use the relative frequency of such affiliative acts between third parties to assess "friendships" between others, which are then taken into account when making behavioural decisions (e.g. Sinha 1998).

However, if the preemption of further attacks was the primary reason for behaving in this manner we might expect that the incidence of post-conflict affiliation between coalition partners would be greater following cases where aid was donated to the recipient, rather than to the perpetrator, of aggression (as retaliatory or opportunistic attacks against former aggressors generally did not occur in this study; chapter 4). Yet there was little indication of any difference in affiliative tendency following cases of victim- versus of aggressor-support. An intriguing possibility is that these interactions instead constitute some form of "payment" for the agonistic aid received, an interpretation which would be consistent with the fact that post-conflict reunions were almost invariably initiated by the beneficiary of the support. Given that opportunities to intervene and provide support may be asymmetrically distributed between coalition partners which differ markedly in size and rank, and given that any support provided by young individuals may be relatively ineffective (e.g. compared to that of adult coalition partners), post-conflict grooming may be a useful alternative enabling immature group members to provide their supporters with an immediate return benefit, and hence encourage the provision of future support. The notion of such reciprocal exchange (or more accurately, interchange: Hemelrijk 1990) of behaviours in nonhumans has proved contentious and difficult to demonstrate rigorously (see de Waal & Luttrell 1988, Seyfarth & Cheney 1988, and Hemelrijk 1996 for discussion of this issue). Nevertheless, two experimental demonstrations of such a phenomenon do exist. In one, female longtailed macaques were shown to be more likely to provide partners with agonistic support - at least of the less costly, aggressor-support variety - after having recently received grooming from the latter (Hemelrijk 1994), whilst in the other, on chimpanzees, an individual (A) was found to be more likely to receive food from another group member (B) if A had previously groomed B (de Waal 1997). In both cases the return favour was contigent upon the occurrence of prior affiliation, and in the latter experiment could be shown to be specific to the service provider - grooming by A had no effect upon sharing by A himself, nor upon sharing by B with others.

# 4

## *Consequences of involvement in aggression*

### *Introduction*

The costs of aggressive acts between conspecifics have traditionally been conceptualised in terms of the physical costs incurred during the encounter itself. Involvement in escalated confrontations can be costly in terms of the time and energy expended, the risk of receiving a debilitating or even fatal injury, and may attract predators at a time when the protagonists are less vigilant than usual (e.g. see Jakobsson *et al.* 1995, Blumstein 1998, regarding the latter point). Theoretical models therefore suggest that the use of escalated aggression should be limited, conflicts of interest instead being resolved via conventions and ritualized displays unless the resource at stake has high value for one or both animals (e.g. Maynard Smith & Price 1973, Maynard Smith & Parker 1976, reviewed in Reichert 1998). However, it is increasingly being realized that the negative consequences of overt aggression may persist well beyond the encounter itself, and that both physical and social penalties are encompassed (de Waal 1986b, de Waal & Aureli 1997).

One physical consequence of agonistic interactions is the activation of a physiological stress response, both prior to (in anticipation of a challenge) and during aggression. This involves the rapid mobilization of stored energy via the release of adrenal hormones, paralleled by increases in heart rate, blood pressure and breathing rate which allow this energy to be utilised effectively. As resources are diverted to cope with the emergency at hand, longer term processes of growth, reproduction and immune function are temporarily inhibited. Under normal circumstances these physiological changes are adaptive, preparing individuals to respond swiftly - whether via flight or counter-attack - to acute stressors such as dangerous situations (reviewed in Gray 1987, Sapolsky 1998). However repeated and chronic overactivation of the stress response can have deleterious effects - being associated with brain damage, circulatory disorders, immunodeficiency and infertility (e.g. Bowman *et al.* 1978, Wasser & Barash 1983, Kaplan 1986, Uno *et al.* 1989, Kaplan *et al.* 1991, von Holst 1998). In social taxa, the altered endocrine profiles which may predispose to such negative health consequences are often found during periods of social instability associated with upheavals in a group's dominance hierarchy, or in the more subordinate individuals within stable hierarchies (Gust *et al.* 1993, Sapolsky 1993, Shively 1998). In such situations the frequent expectation, or actual receipt, of aggression and/or a low degree of control over social events in the aftermath of aggression, may continually re-activate the stress response. Nevertheless, it is not always the lowest-ranking individuals which exhibit the greatest physiological signs of stress or its consequences (see e.g. Packer *et al.* 1995 in primates, and Creel *et*

*al.* 1996 regarding social carnivores), individuals with particular "behavioural styles" may fare better whatever their rank (Virgin & Sapolsky 1997), and the negative effects of acute stressors can often be buffered by adequate social support (e.g. Ray & Sapolsky 1992, Gust *et al.* 1996).

One reason why the physiological preparation produced by the stress response is normally useful is that the risk of being involved in further aggression is a real one. Following an initial conflict, the dominant contestant is less likely to tolerate the proximity of its former opponent in a feeding situation (Cords 1992) and more likely to renew aggression against the latter (Aureli & van Schaik 1991b, Aureli 1992, Silk *et al.* 1996) than under control conditions. Furthermore, in the minutes following a dispute recent victims are also subject to increased rates of attacks from previously uninvolved third parties (Aureli & van Schaik 1991b, Aureli 1992, Castles & Whiten 1998b). This opportunistic harassment by bystanders may be occasioned by the target being in a more vulnerable position than usual due to having recently undergone a "loser experience" (cf. Scott & Fredericson 1951), combined with the possibility that the former aggressor might assist in or at least condone such behaviour. Aggression thus has social costs, which persist beyond the conclusion of the original dispute. In particular, the patterning of interactions between former adversaries may be altered, both in the minutes following the encounter and over subsequent days (see references provided in chapter 3). Former victims appear fearful and avoid the approaches of recent assailants (Cheney *et al.* 1995b, Cheney & Seyfarth 1997), an understandable precaution given the enhanced risk of further aggression. Negative patterns of interaction may even persist over a number of days, with rates of grooming declining and aggression between the opponents increasing over baseline levels (Koyama 1997).

Partly as a consequence of these risks and the need for greater vigilance, recipients of aggression may also incur ecological costs. Obviously, where aggression occurs over access to food or a drinking spot it is usually the subordinate, typically the victim in the contest, which relinquishes or fails to gain possession of the disputed resource. However victims may continue to incur further energetic and foraging costs in the ensuing minutes, as indicated by disturbance to time budgets. So far only two controlled post-conflict studies, on wild long-tailed macaques (*Macaca fascicularis*, Aureli 1992) and wild olive baboons (*Papio anubis*, Castles & Whiten 1998a), have examined this issue. For example, while baboon aggressors spent more time foraging following conflicts former victims did not, and in long-tailed macaques recent victims actually foraged significantly less in the aftermath of aggression when compared with baseline conditions. In both studies recipients of aggression also engaged in more locomotion in the period immediately after conflicts, perhaps due to avoidance of the former opponent or, following contests over food, the need to locate an alternative food source (Aureli 1992).

Finally, contestants typically exhibit elevated rates of self-directed behaviour, such as scratching and autogrooming, in the aftermath of conflicts (de Waal & Yoshihara 1983, Aureli & van Schaik 1991b, Castles & Whiten 1998b, Das *et al.* 1998). Increases in these bodycare activities may in part be due to the circulatory and thermoregulatory changes produced by the exertion of participation in aggression. However, these physiological and behavioural changes may also reflect anxiety on the part of the actor (Maestripieri *et al.* 1992). Administration of anxiety eliciting drugs is known to elevate both heart rate and self-directed behaviour, while anxiolytics diminish the latter (Ninan *et al.* 1982, Moody *et al.* 1988, Schino *et al.* 1996). Increases in heart rate and behaviours such as scratching or self-grooming are also produced in situations likely to be perceived as threatening, for example when a subject is in close proximity to or approached by a higher-ranking conspecific (Troisi & Schino 1987, Pavani *et al.* 1991, Aureli *et al.* 1999, Castles *et al.* 1999). Thus one explanation of the post-conflict rise in self-directed behaviour is that former contestants, particularly victims, are uncertain about their social position and in particular are apprehensive about the possibility of receiving further aggression from others (Aureli *et al.* 1989, Aureli & van Schaik 1991b). Individuals might also be concerned more generally about their relationship with the former adversary; not only whether to expect tolerance or aggression, but also whether or not they can rely on the other's cooperation (for example agonistic support) in the future. The fact that even former aggressors - which are not subject to an increased risk of receiving attacks following conflicts (Castles & Whiten 1998b, Das & van Hooff, in press) - exhibit a post-conflict rise in rates of scratching has been interpreted as suggesting that disturbance to the relationship between opponents is also a source of ongoing anxiety (Aureli 1997, Das *et al.* 1998).

These emotional responses have been proposed to be a mechanism motivating former adversaries to seek one another out and engage in reconciliation (Aureli 1997, Aureli & Smucny, in press). Reconciliation reduces many of the adverse consequences of aggression mentioned above, restoring characteristic levels of tolerance by the dominant individual, diminishing the probability of further attacks against the former victim by either its opponent or third parties, and restoring baseline levels of affiliation between the two combatants (Aureli *et al.* 1989, Aureli & van Schaik 1991b, Cords 1992, Silk *et al.* 1996, Koyama 1997; see chapter 3 for further details). These reunions should therefore diminish a contestant's uncertainty about the future actions of both its opponent and bystanders, and relieve any anxiety it may experience (Aureli & van Schaik 1991b). In this way, reconciliation may more quickly terminate the stress response activated by participation in aggression, and help prevent the negative health consequences associated with prolonged activation. Several pieces of behavioural and physiological evidence are consistent with the notion that reconciliation regulates anxiety levels. These post-conflict reunions are associated with a more rapid decline in self-scratching and in heart rate than

would otherwise occur following aggression (Aureli & van Schaik 1991b, Smucny *et al.* 1997, Castles & Whiten 1998b, Aureli & Smucny, in press). Although affiliative contact with previously uninvolved bystanders also decreases heart rate in the aftermath of conflicts, the decline is faster and more pronounced after reconciliation with the opponent itself (Smucny *et al.* 1997, Aureli & Smucny, in press). Additionally, only reunions involving the former opponents are associated with a significant decline in scratching behaviour, while post-conflict affinitive contacts between aggressors and either relatives of the victim or unrelated bystanders do not have this effect (Das *et al.* 1998). Therefore these changes cannot be attributed to the calming effects of affiliative contact in general, but rather are specific to interactions with one's former opponent. Following rapprochement, attention to the potentially threatening screams of a former attacker, visual monitoring of this individual, and avoidance responses to their approaches, also decline which again suggest a reduction in anxiety on the part of recent victims (Cheney *et al.* 1995b, Cheney & Seyfarth 1997, Koyama 1997).

A recent extension to this Uncertainty Reduction hypothesis (Aureli & van Schaik 1991b) proposes that if a component of the anxiety experienced is due to disturbance of the relationship between former opponents, then contestants should experience greater anxiety following conflicts with more valuable social partners (Aureli 1997). This could provide a proximate explanation for the greater conciliatory tendencies recorded between individuals presumed to possess more valuable relationships (e.g. those with particularly close affiliative bonds and/or exhibiting above-average levels of agonistic support: de Waal & Yoshihara 1983, Aureli *et al.* 1989), and could account for the elevation of reconciliation rates seen following experimentally induced increases in partner value (e.g. Cords & Thurnheer 1993). In ultimate terms, these dyads are thought to display greater tendencies to reconcile due to the potentially greater loss of benefits if such relationships were to be damaged by the occurrence of aggression (Kappeler & van Schaik 1992, de Waal & Aureli 1997). In support of this extended hypothesis, Aureli (1997) found that in captive longtailed macaques aggressive disputes between close associates resulted in greater rates of post-conflict scratching, an indicator of anxiety, in the victim than did conflicts between less affiliated group members; the former class of dyads had previously also been shown to reconcile at higher rates than the latter (Aureli *et al.* 1989). According to the emotional mediation hypothesis then, observed variation in conciliatory tendencies may be created by differences in the level of anxiety provoked in different situations or by different classes of opponent.

This chapter explores the immediate aftermath of unreconciled aggressive confrontations in young rhesus macaques. The consequences of aggression might be particularly important for young cercopithecines, which receive disproportionate amounts of high level aggression (see references provided in chapter 1), and because the negative effects of stressors are known to be particularly pronounced in young mammals (e.g. Stone &

Quartermain 1997); furthermore, sustained stress which occurs during this period of physical growth and brain development can have far-reaching and irreversible effects (Kraemer & Bachevalier 1998, Sapolsky 1998). Whilst physiological and behavioural responses to certain types of social stress (for example that produced by maternal separation: e.g. Laudenslager *et al.* 1990, or by removal from and reintroduction into the natal group: e.g. Gordon & Gust 1993) have been well studied in infant and juvenile macaques, the behavioural and ecological consequences of the normal aggression experienced as part of daily social life have not been systematically investigated in immature primates within a free-ranging population. The initial aim is to document the effects of conflicts upon rates of self-scratching (used as an indicator of anxiety levels), subsequent aggression received, and the distribution of activities within the time budget. These variables will be examined separately in former aggressors and victims, as the physiological, ecological and social consequences of participation in aggression are expected to differ between the two situations, yet only one previous study (which utilised a mixed-age sample: Castles & Whiten 1998a, b) has considered these effects in both roles within the same troop of animals. Secondly, further exploration of two variables frequently found to be associated with significant variation in conciliatory tendency, the context of a conflict and the quality of relationship between the opponents (see chapter 3 and references therein) will be undertaken, in order to investigate whether differences in the likelihood of reconciliation are paralleled by variation in the levels of tension experienced (reflected in rates of self-scratching) as predicted by the emotional mediation hypothesis outlined above (Aureli 1997, Aureli & Smucny, in press).

## *Methods*

Details of the immature subjects utilised and the data collection procedure adopted are provided in chapter 2. Most analyses were based upon the 231 paired PC/MC observations in which neither an affiliative interaction between former opponents nor an attack against a previously uninvolved bystander had taken place at any point in the PC. Previous studies of adult papionines have demonstrated that reconciliation significantly reduces rates of both scratching (Aureli *et al.* 1989, Das *et al.* 1998) and aggression received (Aureli & van Schaik 1991b, Castles & Whiten 1998b) following conflicts, whilst attacks by victims against bystanders can have a similar effect (Aureli & van Schaik 1991b; see also chapter 6). Therefore PC observations containing these events (regardless of whether the first instance fell within the relevant operationally defined "time window" of <200s or <130s respectively - these values being derived in chapters 3 and 6 - or occurred later on within the 10-minute sample) were discarded in order to exclude any influence which these acts might have upon the post-conflict behaviours of interest, and thus to examine the consequences of the conflict itself as far as possible.

Furthermore, as analyses utilised measures either based upon rates of particular behaviours (self-scratching, aggression received) or the proportion of 10 point time samples in which the subject had been engaged in a particular act (time budget analyses), PC/MC pairs in which one or other observation had been truncated before the full 10-minute period had elapsed were also excluded. This precaution was taken because samples were typically truncated toward the end of PC observations, and where the behaviour in question was expected to be particularly elevated in the period immediately following a conflict the inclusion of these truncated PCs might produce spuriously high values, thus biasing in favour of finding a post-conflict increase in that behaviour. A total of 97 focal subjects contributed toward this sample of 231 paired observations.

[1] First, rates of self-scratching and of aggression received by subjects were compared between PC and MC observations to ascertain whether conflicts were associated with any increase in these behaviour patterns, and if so, over what time interval post-conflict rates remained elevated. *Scratching* was defined as a usually repeated movement of the hand or foot, during which the digital tips were rapidly raked across the individual's hair or skin. All occurrences were recorded, and a new bout was scored if ≥5 seconds had elapsed between events or if the subject switched to an alternative form of self-directed behaviour (see Appendix B). *Aggression received* encompassed any of the behaviour patterns defined under the heading "Agonistic behaviour: aggressive" in Appendix B; these events were recorded as for the original conflict and thus a new bout was scored if ≥30 seconds had elapsed before a renewal between the same adversaries, or the subject engaged in a mutually exclusive act (e.g. affiliation with the opponent) in the meantime.

These analyses were based upon a method derived from that of Aureli & van Schaik (1991b). After checking that there was no temporal trend in the mean rate of scratching per minute across the 10 minutes of the MC observations, the baseline mean (of the individual averages) per minute was calculated across the combined 10-minute MC period. The mean rate in each consecutive minute of the PCs was then calculated from the individual averages for each minute, and compared with the 95% confidence intervals of the MC mean, to see whether and over which contiguous minutes PC rates were consistently elevated. Tests comparing the mean rate of scratching per minute in PCs versus MCs were then conducted at the individual level. Comparisons involving rates of behaviour are sensitive to the duration of the observation period, and tests based on rates calculated across the entire (and arbitrary) 10-minute duration of the paired observations could potentially mask any PC increase which was limited to only the first few minutes following conflicts. Therefore tests utilised PC rates calculated from only those minutes in which post-conflict levels of the behaviour in question had previously been shown to be consistently elevated above baseline levels. The MC mean rate per minute was still calculated over the entire 10-minute period, in order to produce the most reliable value possible, and given that no time course in the behaviour was expected in the MCs.

Analyses were initially performed on the overall sample, before investigating whether these results also held within former aggressors, victims, and bidirectional participants, and whether significant differences in rates of post-conflict scratching existed between the three roles. Comparisons of PC versus MC rates were initially performed using values calculated from the post-conflict "time window" applicable to the overall sample. However, before concluding that a comparison proved nonsignificant, any shorter time window specifically applicable to the role in question was also checked. A more stringent, although rather conservative, alpha criterion ($p \leq 0.025$) was employed whenever such a second partially independent test was performed (see chapter 2 for further details). As tests between the 3 roles involved within-individual comparisons, PC rate data could be utilised without control in these latter comparisons. Following the definitions provided in chapter 3, the individual which exhibited the first aggressive act of a conflict was termed the *aggressor*, and the recipient of this initial act was the *victim*. Thus all analyses in which aggressors and victims are treated separately have been restricted to those PC/MC pairs in which the direction of aggression in the original conflict had been unambiguous (i.e. counter-aggression had not occurred). Conflicts during which the initial victim(s) and/or its supporters (if applicable) retaliated aggressively against the initial aggressor were termed *bidirectional.*

[2] Rates of aggression received by subjects (from former opponents and bystanders combined) were examined using a similar procedure. However as aggressive interactions were relatively rare behaviour patterns and thus mean values in any one minute were likely to be both low and very variable, when examining the time distribution of this behaviour the full dataset of 429 (untruncated) PC/MC pairs was initially utilised, in order to provide a more reliable estimate of the individual averages in each minute and thus a less "noisy" PC curve. A total of 108 focal individuals contributed to this wider set of observations. This modification has a drawback in that the duration of any time window of PC elevation derived may be somewhat shorter than in reality, given that some proportion of the PCs used include events such as reconciliation and/or attacks against bystanders, both of which have been demonstrated to hasten the decline of PC levels of aggression received toward baseline values (see references above). Having thus identified an estimated time window within which to conduct PC versus MC comparisons, the actual tests of individual scores were always then limited to the 231 "unadulterated" PC/MC pairs, in order to examine only the effects of the conflict itself.

[3] To investigate the ecological consequences of involvement in conflicts, the maintenance activity of immature subjects was recorded using instantaneous samples collected at 60-second intervals in PC/MC observations. Definitions of the behaviour patterns scored can be located in Appendix B; these activities were subsequently classified into 5 broad categories as follows:

*Social* All social interactions, whether agonistic, affiliative, neutral or sexual in nature.
*Feeding* Handling, processing or mastication of food items (whether chow, vegetation, insects or soil) as part of an ingestive bout, or drinking water.
*Locomotion* Movement (walking, running, climbing, jumping or swimming) within the group or during group travel, excluding locomotion intrinsic to either social interactions or feeding.
*Self-directed behaviour* Scratching, self-grooming, yawning or body-shaking.
*Other* All remaining activities, predominantly involving remaining stationary whilst alert, masticating food stored earlier in cheek pouches, resting or sleeping.

The average proportion of the 10 point time samples in which subjects had been engaged in each of the above activity categories during PC observations was then compared with the equivalent proportion in the corresponding MC observations, at the individual level. Tests were again performed initially upon the overall sample (all 3 roles combined), before checking whether the results obtained also held within both former aggressors and former victims. All tests utilised the entire 10-minute duration of paired observations. Where an initial comparison on the overall sample proved nonsignificant, a correction factor was applied when the same comparison was subsequently performed within the aggressor or victim subsets of data separately. Also, as 4 PC versus MC comparisons were performed in each round (the category "Other" being discarded in order to minimise the number of separate tests undertaken), a correction for multiple tests was deemed appropriate. In both cases the Hochberg (1988) procedure was employed to determine the appropriate significance criterion (see chapter 2 for further details).

[4] Finally, post-conflict rates of scratching were examined following conflicts which differed in either context (being over food versus of no discernible cause) or the quality of relationship between initial contestants (close versus less frequent associates). These particular factors were considered because both had previously been demonstrated to be associated with significant variation in conciliatory tendency (chapter 3), and because in both cases it has been hypothesized that differences in the degree of anxiety or arousal provoked by these particular types of conflict may mediate the observed differences in reconciliation frequency (e.g. Aureli 1997, Castles & Whiten 1998a). Again, all comparisons were within-individual and thus post-conflict data could be utilised without control. However, given that these analyses required finer subdivision of each individual's PC data, the 231 eligible PCs were supplemented via the addition of 10-minute post-conflict intervals extracted from the focal dataset on 37 juveniles, together with those PCs from the PC/MC dataset for which no matched-control had been obtained. Again, only those post-conflict periods which lasted for at least 10 consecutive minutes, and in which no reconciliation between opponent(s) nor aggression against bystanders had been initiated at any point in the observation, were utilised. An additional 287 of the 462 "marker" conflicts from the Focal dataset and 11 of 14 PCs which

possessed no matched-control were eligible, thus providing a total of 529 post-conflict intervals. Further details of the data collection procedure used in the Focal dataset and extraction of the 10-minute post-conflict intervals can be located in chapter 2, whilst an overview of the subjects used and the total "marker" conflicts and PC intervals obtained is provided in Appendix C.

Both the context of the original conflict, and the nature of the relationship between opponents, were defined as in chapter 3. *Food* conflicts were those where the aggression clearly concerned access to a physical resource (forage, chow, or water) and/or the loser relinquished part or all of the resource to its opponent. Aggressive encounters prompted by the victim's proximity to a third party or directly concerning access to a social partner - whereby the loser was forced to move away from and/or terminate interactions with a third party with which the aggressor then affiliated - were classified as *social*. Aggressive incidents in which no obvious context could be discerned were assigned to the category *none*. As in the previous chapter, post-conflict periods following conflicts in which the context had been ambiguous were excluded. Given the low number of individuals which possessed PCs for all 3 conflict contexts (because few individuals possessed data for conflicts over a social partner), the fact that the small number of PCs per individual in the social context made values for this category relatively unreliable, and the fact that all PC categories were to be further subdivided in the present analyses, the category *social* was excluded and the comparison of context therefore limited to the *food* versus *none* categories. Finally, the focal animal and its initial opponent were regarded as *close associates* if either individual fell within the upper quartile of the other party's contact affiliation scores, derived from the group-wide scan data; all remaining subject-opponent pairs were classified as *other* associates.

Comparisons were performed using data from the period in which the PC mean level of the behaviour pattern in question had previously been demonstrated to be elevated above the 95% upper confidence bound of the MC mean; the appropriate interval therefore varied depending upon both the behaviour pattern in question (scratching or aggression received) and the subset of samples being used (e.g. all roles, former aggressors, or former victims). Analyses were initially performed using the overall dataset (all roles combined), although the former aggressor and former victim subsets were also examined separately. Where a significant difference in post-conflict scratching rates was found between two classes of PC, then I also checked whether systematic differences between the two in either the intensity of the original conflict, or in the amount of aggression subsequently received, could instead have been responsible for the observed difference in rates of post-conflict scratching.

All statistical analyses were carried out at the individual level, and unless otherwise specified values provided refer to the mean (± SE) of individual averages. Use of mean

values per individual was felt to be justified in most analyses, as there was little reason to doubt that the data used in this chapter (e.g. rates of scratching) were normally distributed. Nevertheless nonparametric tests were retained to maintain consistency, given that in specific analyses more rigorous assumptions could not always be met (for example, homogeneity of variance might be equal within individuals without necessarily being equal between individuals). All tests were two-tailed, with the significance criterion set at 5% unless a correction was in force; any cases where this more rigorous alpha level was not met have been highlighted in the text. Otherwise, *p*-values of between 0.05 and 0.10 are referred to as nonsignificant trends or tendencies. For each test, *N* refers to the number of individuals included, while the figure or table legend may additionally report the number of PC/MC pairs or PC periods used.

## *Results*

### *Post-conflict scratching rates*

After conflicts, immature subjects exhibited an increased rate of scratching in the 231 post-conflict observations in which neither reconciliation with the opponent nor attacks against third parties had occurred (Figure 4.1). As expected, no temporal trend was discerned in mean rates of scratching over the 10 minutes of the MC observations. The MC value presented is therefore the mean of individual averages (bouts/ min), calculated across all 10 minutes. Although mean scratching rate in the PCs gradually declined toward baseline levels over time, the PC mean nevertheless remained above the 95% upper confidence limit of the MC mean throughout the 10-minute observation period, in the overall sample. Individual mean scratch rates per minute, calculated over the full 10 minutes, were significantly higher under post-conflict than under baseline conditions (PC = 0.27 ± 0.03 bouts/ min, MC = 0.15 ± 0.01; Wilcoxon: $N = 97$, $Z = -4.37$, $p = 0.000$).

#### *Role in previous conflict*

To examine whether former aggressors as well as victims displayed behavioural signs of sympathetic activation in the aftermath of aggressive interactions, the data were then partitioned according to the focal animal's role in the original conflict (Figure 4.2a-c). There were 73 aggressor, 112 victim and 46 bidirectional PC/MC pairs in which neither reconciliation nor aggression by the focal had taken place at any point in the PC. The highest initial post-conflict level of scratching was exhibited by former victims, in which the PC rate per minute remained above the 95% upper confidence interval of the MC mean for the first 6 consecutive minutes, and then again in the 8th minute onwards. The PC values for bidirectional contestants were above the upper confidence interval of the

MC mean in all 10 minutes; the degree of variation seen in the curve probably being due to the relatively small sample of individuals, and of PC observations per individual, available in this subset of the data. Finally, aggressors exhibited PC rates per minute which were only consistently above MC levels for the first 2 minutes, but were also elevated in the 5th and in the final minutes; therefore aggressors appear to exhibit an increase in scratching for only a brief period following conflicts.

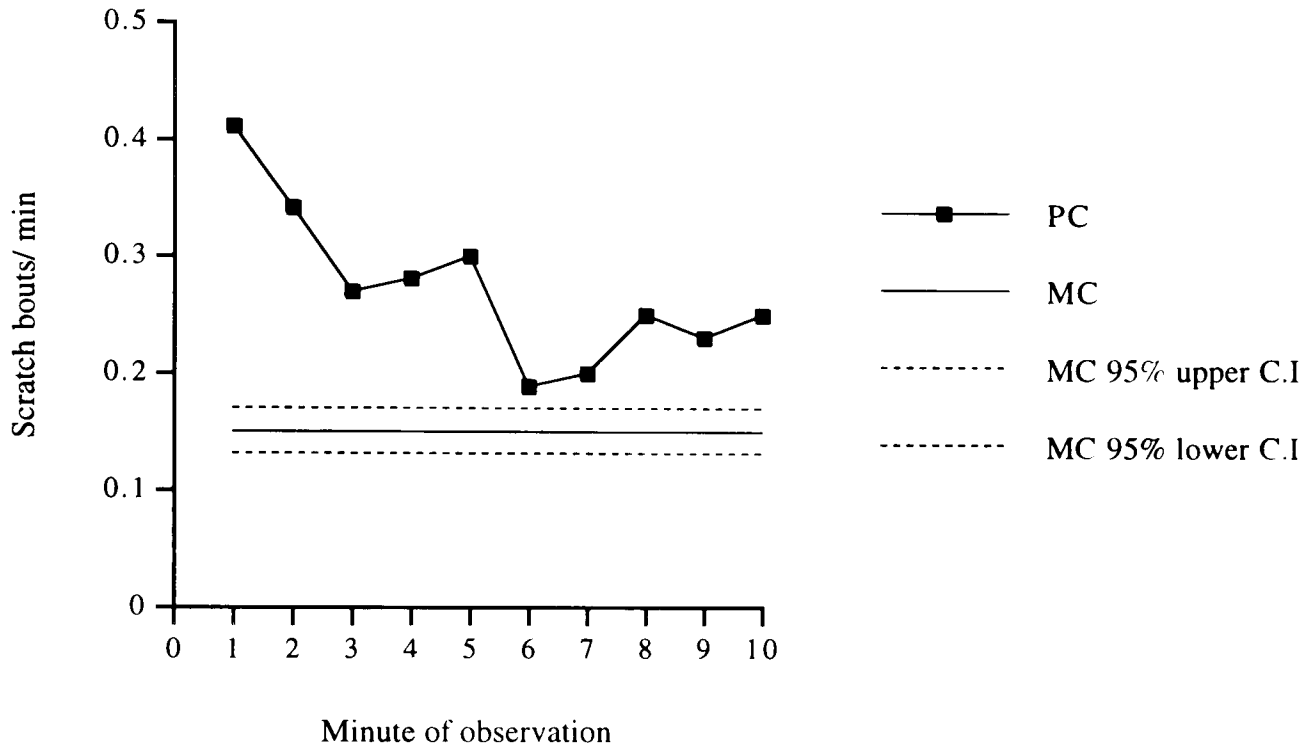
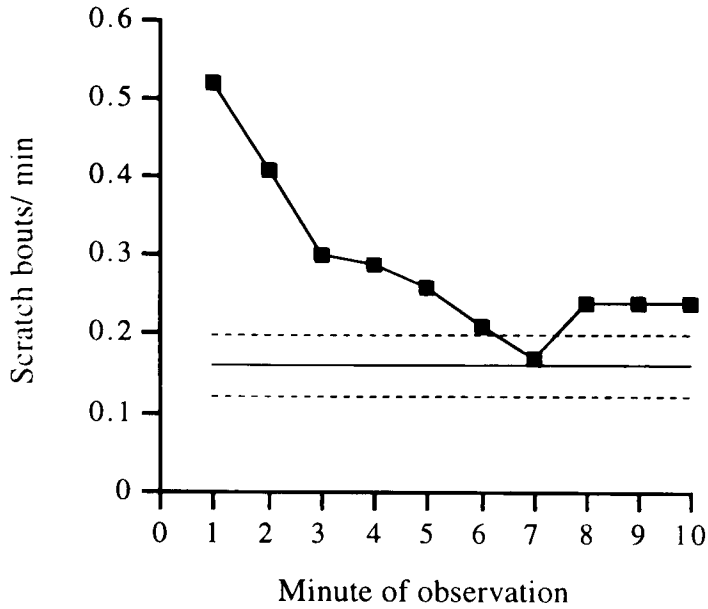



*Figure 4.1.* Scratch rates per minute during post-conflict (PC) observations without reconciliation or initiation of aggression, and matched-control (MC) observations. The PC distribution is the mean of individual averages in each minute; the MC is the mean plus the 95% confidence limits of individual averages over the first 10 minutes. $N = 97$ individuals.

At the individual level, the PC mean scratching rate per minute was significantly greater than control levels when individuals were sampled as victims, and following bidirectional conflicts, but the increase was not significant for former aggressors when rates were calculated over the entire 10-minute observation period (Table 4.1). Restricting the latter comparison to the initial 2 minutes of the PCs (this time window being chosen because PC levels were known to be elevated above the confidence limits of the MC mean during this period in former aggressors), proved significant ($p = 0.029$; Table 4.1). However, the strict significance criterion for use in such a second and partially dependent test would be $p \leq 0.025$, therefore this result should be regarded as only tentative (although in fact the most appropriate alpha level for such a test lies at a point somewhere between $0.025 \leq p \leq 0.05$; see chapter 2 for further details).



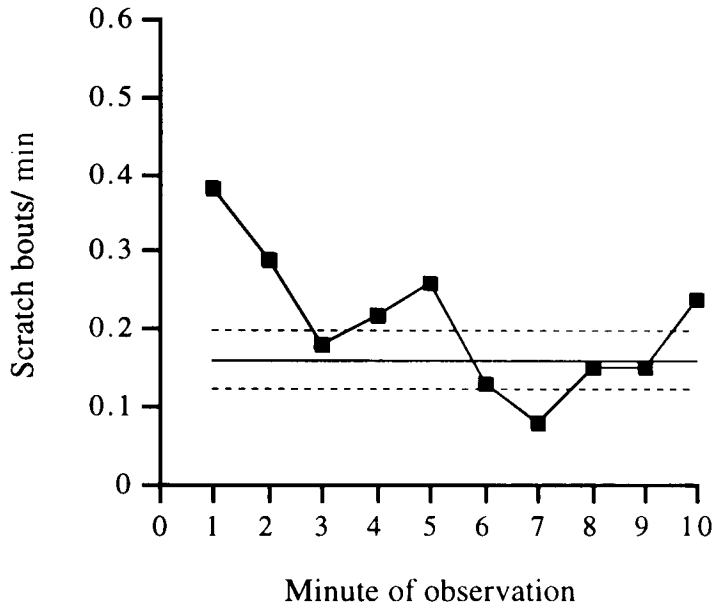

[a] Victim

PC

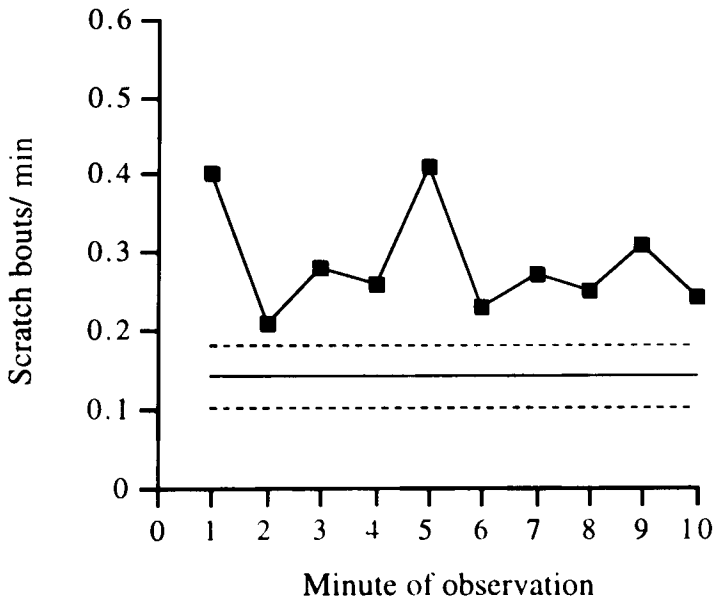
MC

MC 95% upper C.I.

MC 95% lower C.I.




[b] Aggressor




[c] Bidirectional

*Figure 4.2.* Scratch rates per minute during post-conflict (PC) observations without reconciliation or initiation of aggression, and matched-control (MC) observations, according to role in previous conflict. The PC distribution is the mean of individual averages in each minute; the MC is the mean plus the 95% confidence limits of individual averages over the first 10 minutes. $N = 69$, 46 and 39 individuals, respectively.

*Table 4.1.* Comparison of individual mean scratching rate (bouts/ min) in post-conflict versus matched-control observations, according to subject's role in previous conflict. All comparisons refer to Wilcoxon signed-rank tests.

| Sample | Window /s | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| Aggr | 600 | 0.21 ± 0.03 | 0.16 ± 0.02 | 46 | -1.04 | 0.298 NS |
| | 120 | 0.34 ± 0.07 | 0.17 ± 0.04 | 46 | -2.17 | 0.029 |
| Vict | 600 | 0.29 ± 0.03 | 0.16 ± 0.02 | 69 | -3.58 | 0.000 |
| Bidi | 600 | 0.29 ± 0.07 | 0.14 ± 0.02 | 39 | -2.38 | 0.017 |

Only 16 individuals possessed eligible PCs for conflicts of all 3 types. Unsurprisingly, in these individuals there was a significant difference between the 3 roles in post-conflict rates of scratching per minute, calculated over 10 minutes (Figure 4.3; victims = 0.34 ± 0.05 bouts/ min, aggressors = 0.10 ± 0.02, and bidirectionals = 0.29 ± 0.06; Friedman: $N = 16$, $X^2 = 10.72$, df = 2, $p = 0.005$). Exploring the source of this result via post-hoc multiple comparisons specific to the Friedman Analysis of Variance (Siegel & Castellan 1988, pp.180-181) demonstrated that the difference was due to significantly lower PC rates following incidents in which the subject had been the aggressor, there being significant differences between the aggressor and victim conditions ($z = 17.5$, $p < 0.05$) and between the aggressor and bidirectional conditions ($z = 15.0$, $p < 0.05$), but no significant difference between the conditions victim versus bidirectional participant ($z = 2.5$, $p > 0.30$, NS). Furthermore, a difference between roles persisted even when mean rates per minute were calculated using only the initial 2 minutes of the PCs, i.e. the timeframe within which even former aggressors were known to display a significant post-conflict increase over baseline rates (victims = 0.46 ± 0.06 bouts/ min, aggressors = 0.30 ± 0.07, and bidirectionals = 0.34 ± 0.07; Friedman: $N = 16$, $X^2 = 11.28$, df = 2, $p = 0.004$). Again, post-hoc comparisons revealed that the source of this result lay in there being significant differences between the aggressor and victim conditions ($z = 19.0$, $p < 0.05$) and the aggressor and bidirectional conditions ($z = 14.0$, $p < 0.05$), but not between the victim versus bidirectional conditions ($z = 5.0$, $p > 0.30$, NS).

### *Post-conflict aggression received*

The elevated levels of post-conflict scratching observed suggest that subjects experience heightened stress after involvement in conflicts. This stress response should physiologically prepare individuals for the possibility of receiving (or initiating) further aggression, and focal immatures were in fact more likely to become targets of aggression under post-conflict as opposed to baseline conditions. The time distribution of mean bouts of aggression received per minute (from former adversaries and third parties combined) in the 429 untruncated PCs is illustrated in Figure 4.4, demonstrating that PC

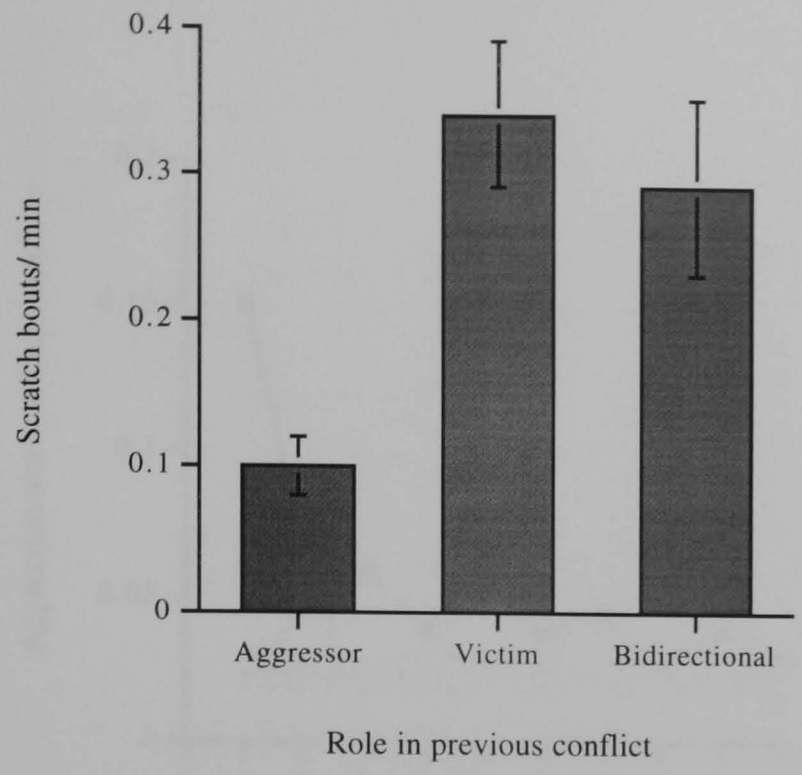



*Figure 4.3.* Mean (± SE) rate of scratching per minute in post-conflict observations without reconciliation or aggression initiated, according to role in previous conflict. Individual means are calculated over entire 10 minute period. $N = 16$ individuals.

values remained above the 95% upper confidence limit of the MC mean for at least the first 7 post-conflict minutes, in the overall dataset. The MC mean rate per minute was again calculated over the entire 10-minute observation, as no time course was expected nor found in the MCs. Utilising the subset of 231 PC/MC pairs without any reconciliation or aggression initiated against bystanders at any point in the PCs produced, as expected, a much more variable PC distribution. Fitting a power curve to the latter in order to better estimate its intercept with the MC 95% upper confidence limit suggested that PC levels first fell to within the MC confidence bounds at approximately 6 minutes (with alternatives, such as exponential or logarithmic curves, all concurring and producing intercepts at between 6 and 7 minutes). Therefore the value of 7 minutes produced from the entire dataset was accepted as a reasonable estimate of the interval during which PC levels of aggression received were elevated.

This effect could be demonstrated at the individual level (PC = 0.055 ± 0.008 bouts/ min over first 7 minutes, versus MC = 0.026 ± 0.004; Wilcoxon: $N = 97$, $Z = -2.77$, $p = 0.006$). Naturally, tests to examine whether PC rates of aggression received were significantly greater than MC rates were performed using only the 231 PC/MC pairs in which no reconciliation or aggression had been initiated at any point in the PC, in order to examine the effects of the original conflict without any influence of these post-conflict events.

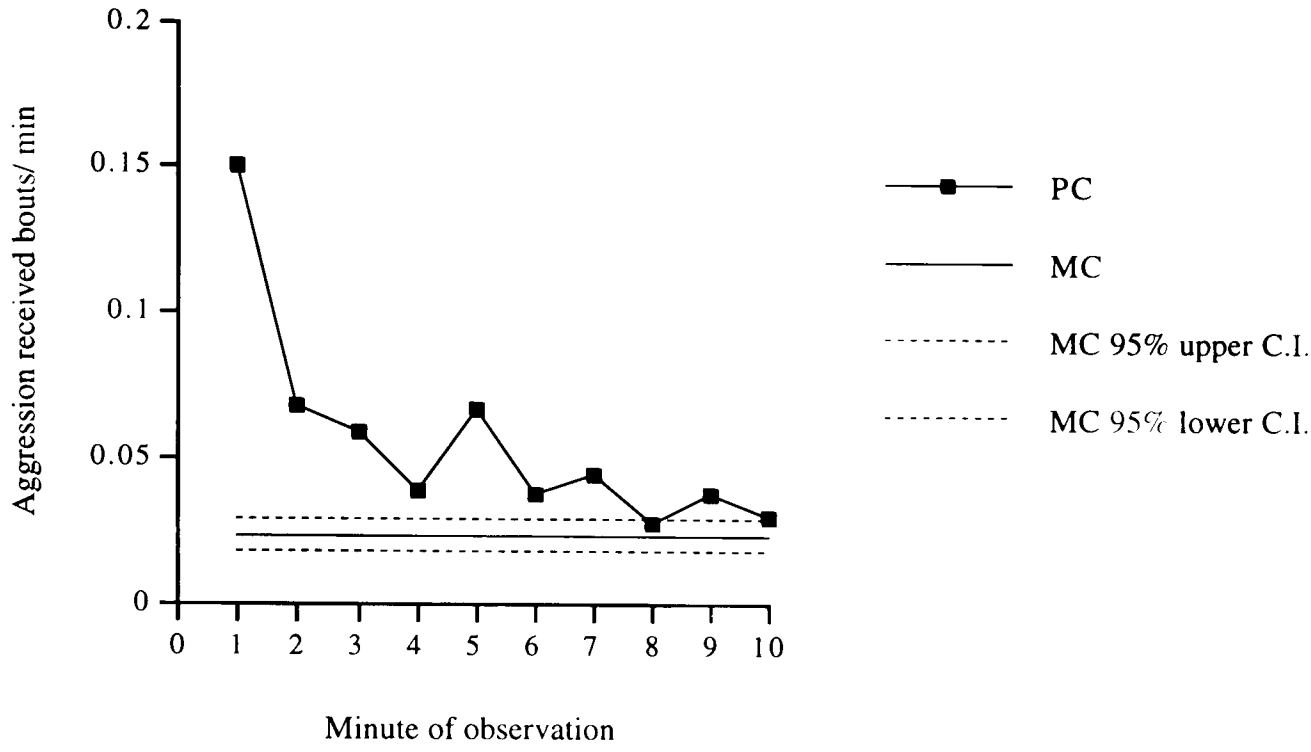



*Figure 4.4.* Rates of aggression received per minute during post-conflict (PC) and matched-control (MC) observations. The PC distribution is the mean of individual averages in each minute; the MC level is the mean plus the 95% confidence limits of individual averages calculated over the first 10 minutes. $N = 97$ individuals.

*Role in previous conflict*

The data were then partitioned according to the focal animal's role in the original conflict (Figures 4.5a-c). Once again former victims exhibited the greatest increase, the mean post-conflict level of aggression received being clearly elevated above the 95% upper confidence limit of the MC mean for the first 3 consecutive minutes and then again between the 5-8th minutes, and broadly declining toward baseline values over time. Bidirectional participants were subject to increased rates of attacks during the first 3 minutes, after which PC values returned to within the confidence limits of the MC mean. Former aggressors did not appear to exhibit any consistent pattern of PC increase, receiving aggression at elevated rates in the first and the final 2 minutes only. However, as the full set of 429 untruncated PC/MC pairs had been used to plot these time distributions, it is possible that the differences were partially due to systematic differences between the 3 roles in other factors likely to affect post-conflict rates of aggression received (such as the likelihood that the subject would initiate an attack against a bystander). Nevertheless, comparisons at the individual level - which utilised only the 231 pairs lacking either reconciliation or aggression initiated against others - also suggested that there was a difference between roles. Whilst former victims received

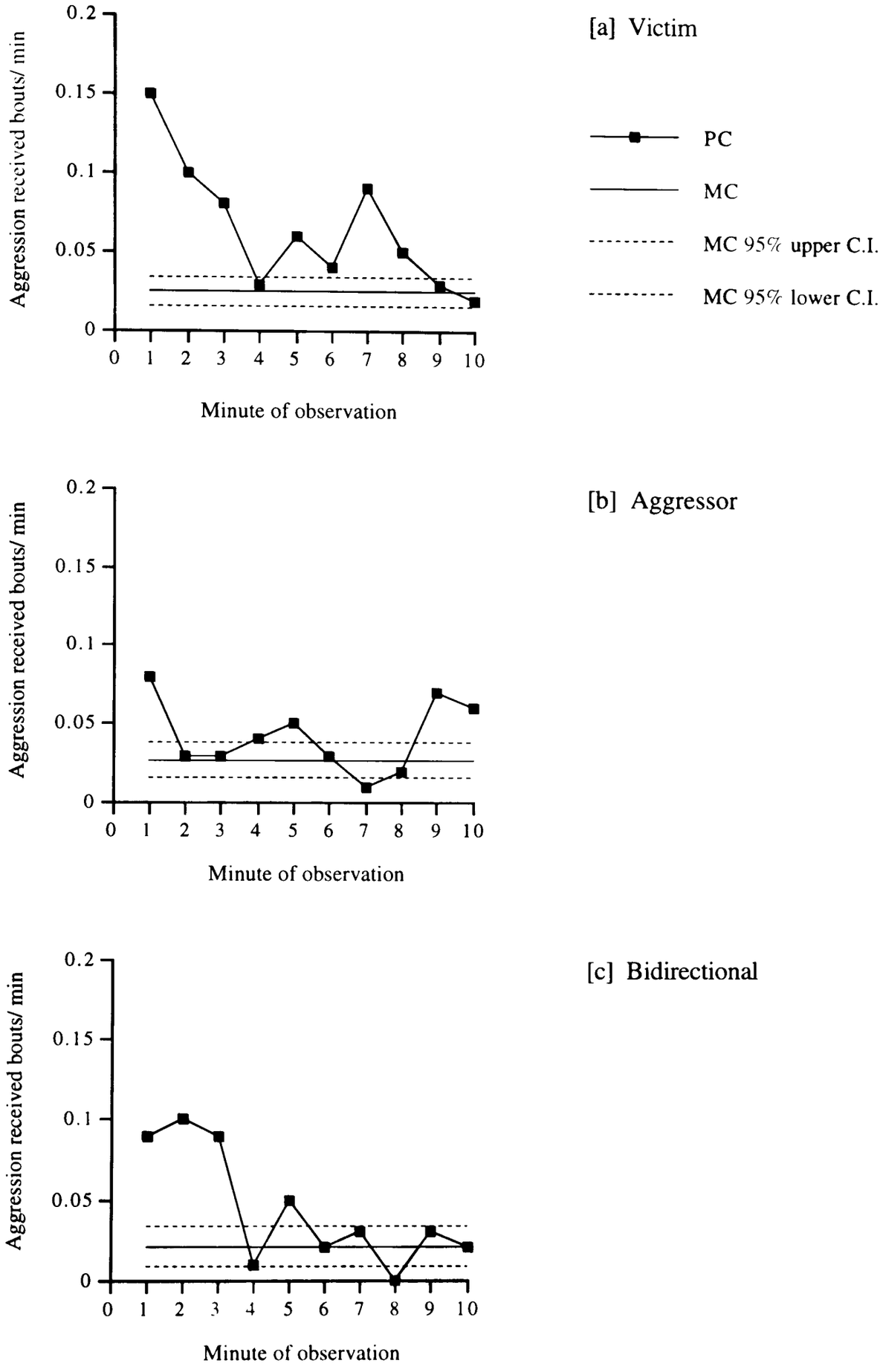



*Figure 4.5.* Rates of aggression received per minute during post-conflict (PC) and matched-control (MC) observations, according to role in previous conflict. The PC distribution is the mean of individual averages in each minute; the MC level is the mean plus the 95% confidence limits of individual averages calculated over the first 10 minutes. $N = 69$, 46 and 39 individuals, respectively.

aggression at significantly elevated rates following conflicts, bidirectional participants and former aggressors did not (Table 4.2). When tests were restricted to the time window relevant to each of the latter 2 roles, a nonsignificant trend toward an increase in the PCs was discerned in bidirectional participants, but this result did not meet the adjustment of the significance criterion required due to performance of a second partially independent test (see methods). Former aggressors did not exhibit any significant increase in aggression received, even when the comparison was limited to only the first minute following conflicts.

*Table 4.2.* Comparison of individual mean rate of aggression received (bouts/ min) in post-conflict versus matched-control observations, according to subject's role in previous conflict. All comparisons refer to Wilcoxon signed-rank tests.

| Sample | Window /s | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* | |
|---|---|---|---|---|---|---|---|
| Aggr | 420 | 0.040 ± 0.010 | 0.025 ± 0.007 | 46 | -0.97 | 0.330 | NS |
| | 60 | 0.096 ± 0.034 | 0.025 ± 0.007 | 46 | -1.49 | 0.136 | NS |
| Vict | 420 | 0.067 ± 0.011 | 0.027 ± 0.005 | 69 | -2.79 | 0.005 | |
| Bidi | 420 | 0.032 ± 0.011 | 0.027 ± 0.010 | 39 | -0.21 | 0.836 | NS |
| | 180 | 0.050 ± 0.018 | 0.027 ± 0.010 | 39 | -1.73 | 0.084 | NS |

Although the degree to which levels of aggression received from others were elevated over baseline levels had depended upon a subject's role in the previous conflict, there was no significant difference overall between the 3 roles when PC rates of aggression received over the initial 7 minutes were directly compared in the 16 individuals which possessed samples of all 3 types (Fig. 4.6; aggr = 0.011 ± 0.001 bouts/ min, bidi = 0.037 ± 0.014, vict = 0.066 ± 0.021; Friedman: $N = 16$, $X^2 = 2.84$, df = 2, $p = 0.241$, NS). However, pairwise comparisons between the 3 categories revealed that there was a tendency for individuals to receive more threats and attacks over this period when they had been victims as opposed to aggressors (Wilcoxon tests: aggr vs vict: $Z = -2.25$, p = 0.024), but that neither role differed appreciably from instances where the subject had participated in a bidirectional conflict (aggr vs bidi: $Z = -1.44$, $p = 0.151$, NS, vict vs bidi: $Z = -1.12$, $p = 0.263$, NS). Again, the difference between aggressors and victims has to be interpreted with caution, as the result did not meet the correction factor of $p < 0.017$ which was required in this instance.

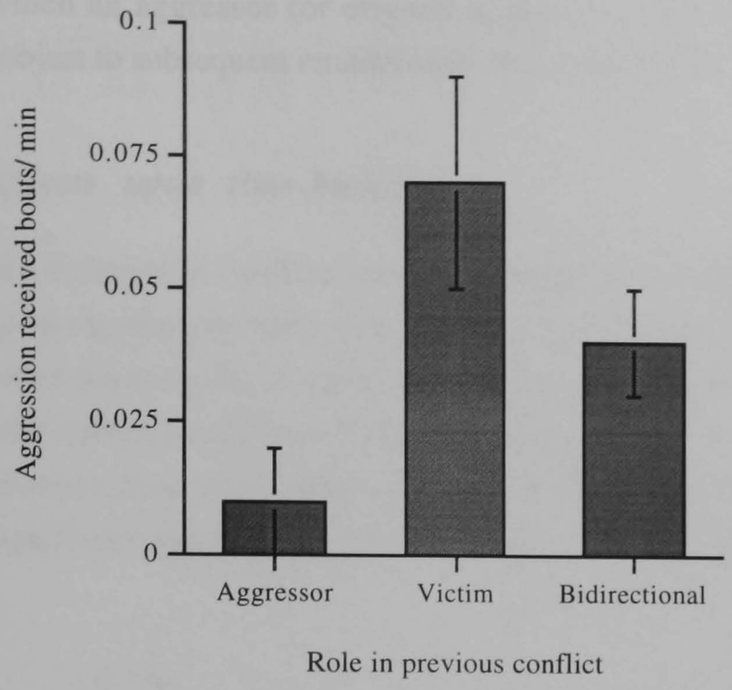



*Figure 4.6.* Mean (± SE) rate of aggression received per minute in post-conflict observations without reconciliation or aggression initiated, according to role in previous conflict. Individual means are calculated over the initial 7 post-conflict minutes (see text for explanation). $N = 16$ individuals.

### *Aggression received from former opponents*

Finally, examination of the subset of interactions comprising aggression received specifically from former opponents produced results consistent with the overall pattern described above. Subjects received significantly more aggression from former adversaries in the first 7 minutes of post-conflict observations than in the corresponding MC observations (PC = 0.0085 ± 0.0035 bouts/ min, MC = 0.0003 ± 0.0003; Wilcoxon: $N = 97$, $Z = -2.78$, $p = 0.005$), although such renewals were infrequent. It should be noted that these figures underestimate the total frequency of renewed aggression following conflicts, given that this analysis did not additionally consider those bouts of aggression which were initiated by focal subjects.

This increase in aggression received from opponents remained significant even if the analysis was restricted to those PC/MC pairs in which the distance between initial opponents at the beginning of the MC observation equalled, or was actually less than, that at the commencement of the matching PC (see chapter 3 for the distance categories utilised; Wilcoxon: $N = 87$, $Z = -2.50$, $p = 0.013$). Therefore the constraints of inter-opponent distance were not responsible for the significantly lower levels of aggression recorded under baseline conditions. It was notable that the risks of renewed aggression essentially seemed to be borne by victims - in the entire dataset, only 4 of the 41 post-conflict bouts of further aggression recorded between former opponents were cases in

which an aggressor (or original aggressor, if the conflict had been bidirectional) was subject to subsequent retaliation by its former victim.

### *Effects upon time-budgets*

Involvement in conflicts also had ecological consequences (Fig. 4.7). Focal immatures spent significantly more time, measured as the mean proportion of point time samples per observation, in locomotion and self-directed behaviour under post-conflict as compared with control conditions (Table 4.3; taking into account corrections for multiple tests). In contrast, time spent feeding decreased significantly following conflicts. There was no significant change in the proportion of time spent in social interaction.

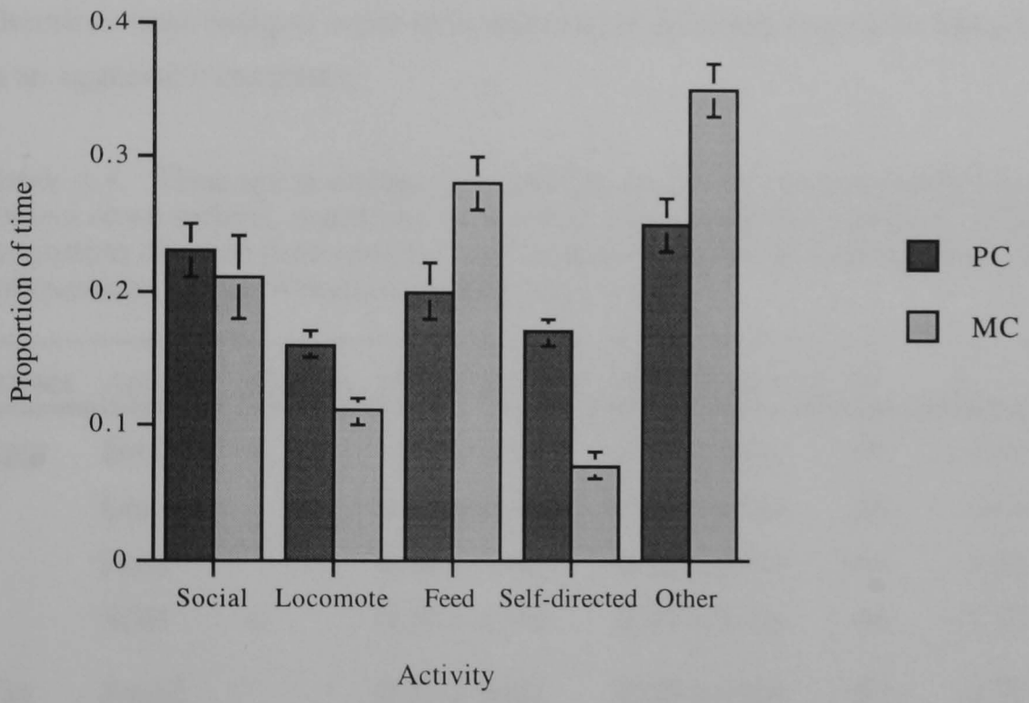



*Figure 4.7.* Activity budgets in 10 minute post-conflict (PC) and matched-control (MC) observations; mean (± SE) proportion of time spent in 5 maintenance activities. $N = 97$ individuals.

*Table 4.3.* Time spent engaged in specific activities in post-conflict versus matched-control observations. Values refer to the proportion of point time samples, conducted at 60-second intervals, per observation. All comparisons utilise Wilcoxon signed-ranks tests.

| Activity | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* | |
|---|---|---|---|---|---|---|
| Social | 0.23 ± 0.024 | 0.21 ± 0.025 | 97 | -1.17 | 0.244 | NS |
| Locomotion | 0.16 ± 0.011 | 0.11 ± 0.008 | 97 | -3.92 | 0.000 | |
| Feeding | 0.20 ± 0.018 | 0.28 ± 0.021 | 97 | -2.90 | 0.004 | |
| Self-directed | 0.17 ± 0.015 | 0.07 ± 0.009 | 97 | -5.85 | 0.000 | |

To examine whether former aggressors or victims were responsible for this pattern of results, data from unidirectional conflicts were then partitioned according to the focal animal's role in the original conflict (Fig. 4.8a-b). Individuals spent significantly more time engaged in self-directed behaviour following conflicts, both when they had been aggressors and when victims (Table 4.4). However, although both roles exhibited changes in the same direction when the proportions of time spent in locomotion (an increase) or feeding (a decrease) were examined, these shifts were more marked and only reached significance following conflicts in which subjects had been the target of aggression. Finally, the lack of any demonstrable effect of conflicts upon time spent in social interaction in the overall sample was revealed to be due to a difference in response between former aggressors and victims; individuals exhibited a significant increase following the former type of conflict and a nonsignificant decline if in the latter role. Therefore time-budgets seem to be affected in different ways depending upon one's role in an aggressive encounter.

*Table 4.4.* Time spent engaged in specific activities in post-conflict versus matched-control observations, according to subject's role in previous conflict. Values refer to the proportion of point time samples, conducted at 60-second intervals, per observation. All comparisons utilise Wilcoxon signed-ranks tests.

| Subset | Activity | Change | PC Mean ± SE | MC Mean ± SE | *N* | *Z* | *p* | |
|---|---|---|---|---|---|---|---|---|
| Aggr | Social | + | 0.31 ± 0.047 | 0.19 ± 0.044 | 46 | -2.58 | 0.010* | |
| | Loco'n | | 0.14 ± 0.018 | 0.12 ± 0.018 | 46 | -1.06 | 0.290 | NS |
| | Feed | | 0.20 ± 0.031 | 0.25 ± 0.028 | 46 | -1.58 | 0.113 | NS |
| | SDB | + | 0.13 ± 0.019 | 0.07 ± 0.018 | 46 | -2.67 | 0.008 | |
| Vict | Social | | 0.21 ± 0.033 | 0.25 ± 0.034 | 69 | -0.90 | 0.367 | NS |
| | Loco'n | + | 0.18 ± 0.017 | 0.11 ± 0.015 | 69 | -3.14 | 0.002 | |
| | Feed | - | 0.20 ± 0.023 | 0.27 ± 0.029 | 69 | -2.19 | 0.029 | |
| | SDB | + | 0.20 ± 0.022 | 0.07 ± 0.012 | 69 | -4.60 | 0.000 | |

*As the initial comparison (in the overall dataset) for this behaviour category had been nonsignificant the significance criterion applied was halved for the purposes of this second, only partially independent, test.

Inspection of figures 4.7 and 4.8 revealed that the mean proportion of time spent in the activity category "Other" in PCs was substantially lower than the MC mean proportion, both in the overall sample and when the dataset was split according to the subject's role in the previous conflict. However, three of the constituent behaviour patterns - "gnaw object", "manipulate object" and "visual scan" (see behavioural definitions in Appendix B) - stood out in that completely the opposite pattern could be discerned in the

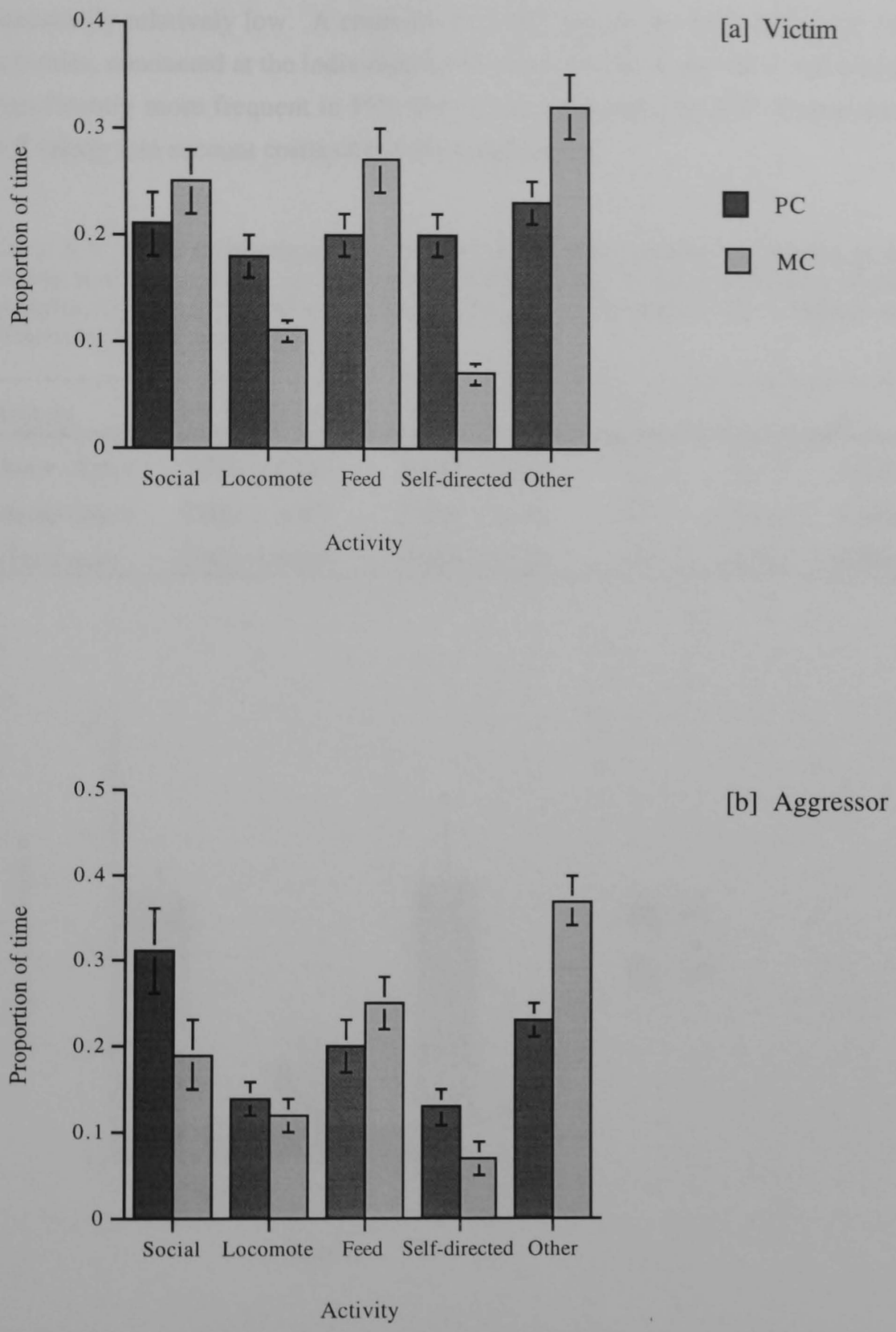



*Figure 4.8.* Activity budgets of [a] unilateral victims and [b] unilateral aggressors in 10 minute post-conflict (PC) and matched-control (MC) observations; mean (± SE) proportion of time spent in 5 maintenance activities. $N$ = 69 and 46 individuals, respectively.

summarised data (Figure 4.9), although the figures for these individual activities were necessarily relatively low. A comparison of PC versus MC proportions for these three activities, conducted at the individual level, revealed that in each case the behaviour was significantly more frequent in PCs than in the corresponding MC observations (Table 4.5; taking into account corrections for multiple tests).

*Table 4.5.* Time spent engaged in three environment-oriented activities in post-conflict versus matched-control observations. Values refer to the proportion of point time samples, conducted at 60-second intervals, per observation. All comparisons utilise Wilcoxon signed-ranks tests.

| Activity | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|
| Gnaw object | 0.018 ± 0.005 | 0.003 ± 0.001 | 97 | -3.47 | 0.001 |
| Manip object | 0.048 ± 0.007 | 0.006 ± 0.002 | 97 | -5.60 | 0.000 |
| Visual scan | 0.051 ± 0.011 | 0.009 ± 0.002 | 97 | -4.74 | 0.000 |

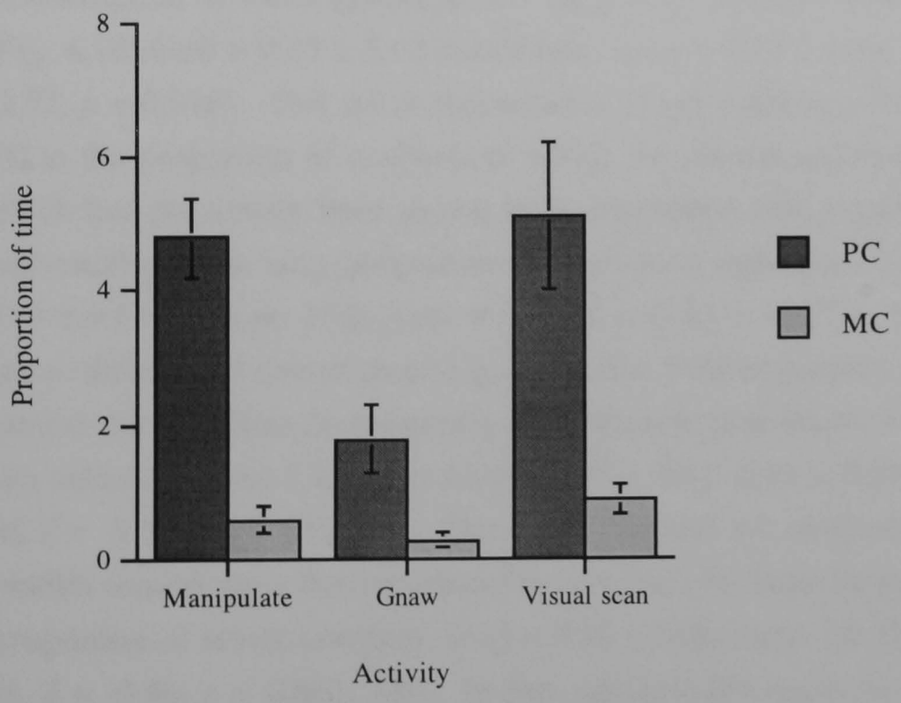



*Figure 4.9.* Activity budgets in 10 minute post-conflict (PC) and matched-control (MC) observations; mean (± SE) proportion of time spent in 3 environment-oriented activities. $N = 97$ individuals.

In all three cases, individuals exhibited a post-conflict increase both when they had been the perpetrator of aggression in the original conflict and when they had been the target (Table 4.6).

*Table 4.6.* Time spent engaged in three environment-oriented activities in post-conflict versus matched-control observations, according to subject's role in the previous conflict. Values refer to the proportion of point time samples, conducted at 60-second intervals, per observation. All comparisons utilise Wilcoxon signed-ranks tests.

| Subset | Activity | PC Mean ± SE | MC Mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| Aggr | Gnaw object | 0.016 ± 0.0076 | 0.001 ± 0.0011 | 46 | -2.11 | 0.035 |
| | Manip object | 0.048 ± 0.0127 | 0.007 ± 0.0033 | 46 | -3.34 | 0.001 |
| | Visual scan | 0.034 ± 0.0098 | 0.007 ± 0.0033 | 46 | -2.70 | 0.007 |
| Vict | Gnaw object | 0.022 ± 0.0081 | 0.004 ± 0.0022 | 69 | -2.10 | 0.036 |
| | Manip object | 0.052 ± 0.0093 | 0.005 ± 0.0023 | 69 | -4.32 | 0.000 |
| | Visual scan | 0.047 ± 0.0140 | 0.010 ± 0.0039 | 69 | -3.14 | 0.002 |

### *Effect of conflict context upon post-conflict increase in scratching*

Focal subjects scratched significantly less often following conflicts over food than after conflicts with no obvious cause ("none"), in 10-minute PC intervals in which no reconciliation between opponents nor aggression against bystanders had been initiated (Fig. 4.10; food = 0.19 ± 0.03 bouts/ min, none = 0.25 ± 0.02; Wilcoxon: $N = 46$, $Z = -2.57$, $p = 0.010$). This result was not due to any difference between the two types of PC in the proportion of conflicts in which the subject had been the aggressor, a role which had previously been shown to be associated with significantly lower levels of post-conflict scratching (proportion of conflicts as aggressor: 0.34 ± 0.06 for food PCs, 0.33 ± 0.05 for none; Wilcoxon: $N = 46$, $Z = -0.32$, $p = 0.746$, NS). Nor was the result due to differential risk of receiving aggression from opponents and bystanders; conflict context did not affect the mean rate of aggression received per minute in the PCs (bouts/ min calculated over 7 minutes: food = 0.05 ± 0.01, none = 0.05 ± 0.01; Wilcoxon: $N = 46$, $Z = -0.59$, $p = 0.556$, NS). The result was also not confounded by any influence of conflict context upon the intensity of the conflict, the latter being defined as in chapter 3 (proportion of severe conflicts: food = 0.50 ± 0.06, none = 0.53 ± 0.04; Wilcoxon: $N = 46$, $Z = -0.40$, $p = 0.692$, NS). In fact, subjects did not scratch more following high intensity conflicts than after mild aggression anyway (high: 0.23 ± 0.02 bouts/ min calculated over 10 minutes, low: 0.20 ± 0.02; Wilcoxon: $N = 63$, $Z = -0.82$, $p = 0.414$, NS). Therefore there appears to be a genuine difference in the amount of scratching provoked by the two types of conflict, with confrontations over food producing significantly lower levels of subsequent self-scratching.

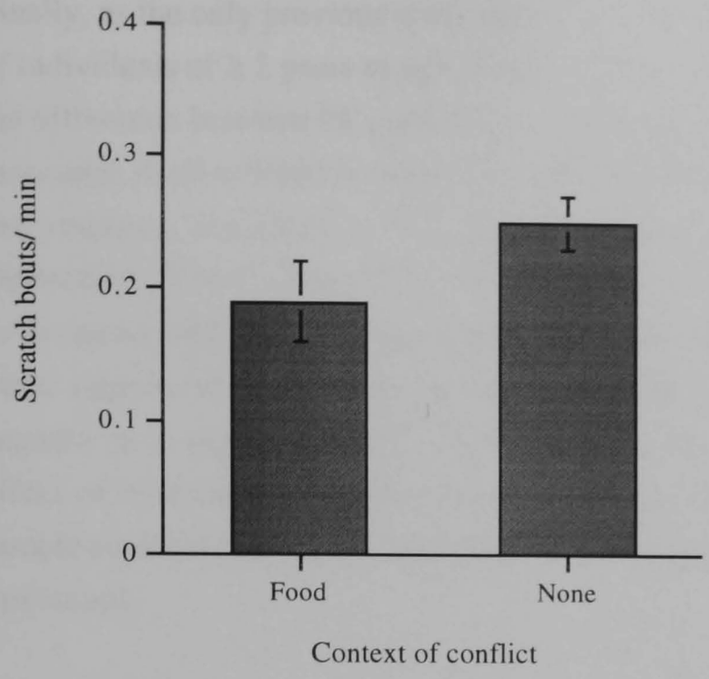



*Figure 4.10.* Mean (± SE) rate of scratching per minute in post-conflict periods without reconciliation or aggression initiated, according to context of previous conflict. $N = 46$ individuals.

### *Effect of relationship quality upon post-conflict increase in scratching*

Immature subjects did not scratch more often following conflicts with opponents with whom they had a strong affiliative bond than after conflicts with less frequent associates (close associates: 0.21 ± 0.03 bouts/ min calculated over 10 min, other associates: 0.20 ± 0.02; Wilcoxon: $N = 47$, $Z = -0.33$, $p = 0.739$, NS). Nor could any difference be discerned when former aggressors and former victims were examined separately, using data from the time window of PC elevation relevant to the role being considered (aggressors, bouts/ min calculated over initial 2 min: 0.17 ± 0.05 versus 0.23 ± 0.04; Wilcoxon: $N = 17$, $Z = -0.91$, $p = 0.363$, NS; victims, calculated over initial 6 min: 0.22 ± 0.04 versus 0.19 ± 0.02; Wilcoxon: $N = 30$, $Z = -0.07$, $p = 0.946$, NS). The comparison remained nonsignificant even when performed using only the "non-food" conflicts (i.e. excluding those over food or of ambiguous context), on the grounds that post-conflict rates of scratching were known to be lower following conflicts over food (over 10 min: close = 0.23 ± 0.04, other = 0.21 ± 0.02; Wilcoxon: $N = 37$, $Z = -0.37$, $p = 0.712$, NS). Even when the comparison was restricted to PCs taken from the PC/MC dataset alone (i.e. the dataset in which a significant difference in conciliatory tendency between these two types of conflict had previously been demonstrated), no difference was present (close: 0.21 ± 0.04, other: 0.22 ± 0.03; Wilcoxon: $N = 29$, $Z = -0.32$, $p = 0.746$, NS).

Finally, as the only previous study examining this issue had been conducted on a sample of individuals of ≥ 2 years in age (Aureli 1997), I also checked whether the magnitude of the difference between PC scratch rates following conflicts with close versus with other associates itself differed between age cohorts, a difference perhaps not being apparent in the youngest immatures. Not only was there no significant association with age (Spearman: $N = 47$, $r_S = -0.07$, $p = 0.632$, NS), but no consistent pattern was apparent in the mean values for each age cohort; the sign of the mean difference between close and other opponents in PC scratch rates was positive in yearlings and 3-year-olds, but negative in 2- and 4-year-olds. Therefore there was no indication that the absence of any effect of relationship quality upon post-conflict rates of self-scratching in the overall sample could have been due to such an effect being present but restricted to only the older immatures.

## *Discussion*

Immature macaques exhibited a clear stress response, indexed by elevated rates of self-scratching, following involvement in aggressive confrontations. The necessity of physiological preparation for subsequent aggression was corroborated by the fact that subjects were more likely to become the target of further attacks, both from their former opponent and from previously uninvolved third parties, in the minutes following a conflict. Ecological costs also appear to be incurred, given the reduction in the proportion of time spent feeding and the increase in time spent in locomotion observed under post-conflict conditions. The above costs were predominantly borne by the recipient of aggression, although even former aggressors displayed some increase in behaviours likely to be indicative of tension, such as self-directed and object-oriented displacement activities. Finally, post-conflict scratch rates were significantly lower following disputes involving food items, as opposed to those with no discernible context. However, conflicts between particularly close associates were not followed by significantly higher levels of scratching than were those between less favoured social partners. These results suggest that differential anxiety, which rates of self-directed behaviour are presumed to reflect, may mediate some of the commonly observed variation in conciliatory tendency following aggression (namely that associated with the context of a conflict), yet other differences in reconciliation rates (e.g. that due to variation in the quality of relationship between the former combatants) appear to be achieved in the absence of any demonstrable difference in levels of post-conflict stress.

*Receipt of aggression*

Involvement in aggressive encounters clearly entailed physical costs beyond the immediate risks and expenditure of time and energy inherent in the original bout. Most obviously, contestants were more likely to receive further aggression in the minutes following conflicts (after which neither reconciliation nor attacks against bystanders had taken place) than at other times. The degree of risk, however, appeared to depend upon an animal's role in the previous altercation; former victims were subject to elevated levels of aggression following conflicts (and bidirectional participants exhibited a trend in this direction), whilst former aggressors were not. These results mirror those of previous studies of papionines utilising mixed-age samples, in which victims have been reported to receive further attacks (e.g. de Waal & Yoshihara 1983, Aureli *et al.* 1989, Aureli & van Schaik 1991b, Aureli 1992, Cords 1992) whilst aggressors were not subject to such a post-conflict increase (Cords 1992, Das & van Hooff, in press), although only in one previous study were both roles examined in the same population (Castles & Whiten 1998b). Although attacks were not specifically partitioned according to the perpetrator's association with the contestants, the absence of any appreciable post-conflict increase in the levels of aggression received by former aggressors suggests that post-conflict retaliation by the relatives or high-ranking supporters of victims does not commonly occur in this population, at least not in the 10 minutes immediately following a dispute.

A proportion of these attacks were performed by the original adversary, an outcome which was selective to former opponents and was not merely due to differences between post-conflict and matched-control observations in the likelihood that these individuals would be in proximity. This result concurs with previous findings that interactions between former opponents are affected in a negative manner following unreconciled disputes (Aureli *et al.* 1989, Aureli & van Schaik 1991b, Aureli 1992, Cords 1992, Silk *et al.* 1996, Koyama 1997). Such renewals were infrequent, but mirrored the overall pattern of aggression received in that most antagonism reflected the direction of the original conflict; aggressors were very rarely the targets of subsequent retaliation from their former victims. This disparity between roles was probably due to the fact that the initial instigator of aggression typically outranked the recipient, and in rhesus macaques retaliation counter to the dominance hierarchy is comparatively rare (see e.g. Bernstein *et al.* 1983b, Thierry 1986, de Waal & Luttrell 1989). Renewed attacks might simply represent a continuation of what is - in the animals' view - the same conflict, although it is possible that the likelihood of their occurrence might be determined by the manner in which the original dispute terminated. For example, individuals might be more likely to re-attack following incidents in which the loser had not acknowledged the winner's superiority by submitting formally (cf. de Waal & Luttrell 1985, de Waal 1986a), or had not deferred sufficiently quickly.

However, the majority of post-conflict aggression received appeared due to previously uninvolved bystanders. Attacks against recent victims, sometimes even culminating in "mobbing" by multiple individuals, have long been reported in macaques (e.g. Bernstein & Gordon 1974). A possible explanation for these opportunistic attacks is that the post-conflict situation provides an opportunity to attempt to reinforce or reverse an existing dominance relationship with the target at relatively low cost. By choosing this moment to attack, the bystander may benefit if the target is distracted due to the need to monitor its former opponent, and the bystander's actions may be more likely to receive active support from the latter. This may have additional benefits for the assailant, which may thereby strengthen its own bonds with the former aggressor (Aureli & van Schaik 1991b). Perhaps more importantly, an individual which has recently lost a conflict may be more easily beaten than under other circumstances, a phenomenon termed the "loser effect" (reviewed in Chase *et al.* 1994, Hsu & Wolf 1999). Research in a broad range of vertebrates has documented a tendency for an animal which has been defeated in one contest to then lose in a subsequent interaction with an *otherwise equally matched* individual. In some cases, prior losers are at a disadvantage even against considerably smaller opponents - ones which they would normally be expected to defeat easily in any other dyadic encounter (e.g. in birds: Drummond & Osorno 1992). Although comparable experiments do not appear to have been carried out in primates, the patterning of agonistic interactions during experiments in which novel triads of individuals were convened was at least consistent with the operation of a loser effect in rhesus macaques (Mendoza & Barchas 1983, Mendoza 1993; see further description in chapter 6). A possible mechanism involves the physiological changes known to occur in many primates following agonistic encounters and the formation of dominance relationships, in particular a decline in plasma androgen levels following a defeat (Rose *et al.* 1972, Rose *et al.* 1975). Transient suppression of circulating testosterone to below a threshold level may diminish an individual's readiness to participate in aggression, and/or the intensity and persistence of its responses when challenged. These physiological alterations might be adaptive in cases where an individual therefore refrains from initiating fights at a time when its energy levels are low, or is prevented from repeatedly engaging in aggression with an individual to whom it is likely to lose. However bystanders which pay attention to conflicts between other group members (see chapter 6 and references therein) can take advantage of these changes, and may gain a temporary advantage over recent victims.

*Ecological consequences*

The post-conflict alterations observed in time budgets suggest that recent victims additionally incur energetic costs which persist beyond the conclusion of the encounter itself. After receiving aggression subjects spent significantly more time in locomotion, and less time feeding, than under baseline conditions; responses similar to those already

documented in wild longtailed macaques and olive baboons (Aureli 1992, Castles & Whiten 1998a). The increase in locomotion following unreconciled conflicts might simply reflect the physiological and psychological stress provoked by involvement in aggression, responses which may be exhibited by both contestants but are typically more pronounced and longer lasting in the victim (see below). In young animals changes in ambulatory behaviour are often associated with situations which produce arousal or distress - for example the amount of time spent moving (or conversely, resting) is altered in infant macaques following separation from their mothers (Hinde & Spencer-Booth 1971, Laudenslager *et al.* 1990). Following aggression, however, active avoidance of former opponents or other potentially dangerous groupmates (see section above) may contribute to the increase in locomotor activity exhibited by victims. For example, results obtained in wild longtailed macaques were consistent with the interpretation that increased locomotion in the first few minutes after receiving aggression was associated with keeping the former aggressor at a distance (Aureli 1992), while Cheney & Seyfarth (1997) have shown that following unreconciled conflicts wild chacma baboons appear fearful and become more likely to move away in response to approaches from their former attackers. This increase in activity appears to be confined to movement within the group; there was no indication in either this study or those by Aureli (1992) and Castles & Whiten (1998a) that conflicts caused former victims to temporarily abandon their group. Of 455 post-conflict observations, only in a handful of instances was an immature subject observed to leave its current group, and then only to walk directly to another subgroup where it immediately joined an older sibling or adult male affiliate. This is to be expected, as in the wild predation risk is likely to limit the option of simply leaving a group, and small size and inexperience render young animals particularly vulnerable to this danger (reviewed in Janson & van Schaik 1993). Predators are absent at this study site, but lone individuals - especially immatures - are nevertheless exposed to high rates of aggression from neighbouring groups of conspecifics (pers. obs.). Furthermore, temporary abandonment of one's group cannot effectively remove one of the presumed causes of a victim's agitation, namely the uncertainty about its future treatment by its former adversary or other group members.

The proportion of time spent feeding was reduced in both aggressors and victims following conflicts, but only significantly so in the latter. In part this may be a direct effect of feeding competition; a proportion of the conflicts observed arose over access to food or water and in these the recipient of aggression was typically prevented from obtaining or forced to relinquish the disputed resource. Thus the loser would necessarily need to pause before attempting to return to the same location, or would need to seek an alternative source of food (cf. Aureli 1992). Such an explanation would equally account for the finding, in the only previous study to examine post-conflict time budgets in aggressors, that former aggressors actually exhibited an increase in time spent foraging

relative to baseline conditions (Castles & Whiten 1998a). However, in the current study aggressors did not exhibit a comparable increase in feeding time, and the vast majority of initial conflicts did not concern food (see chapter 3). Perhaps an even more likely explanation is that the need for enhanced vigilance reduces the ability of recent victims to perform tasks which require sustained attention (such as foraging and grooming, both commonly regarded as incompatible with effective vigilance: van Schaik & van Noordwijk 1989, Maestripieri 1993). This may be occasioned primarily by the need to guard against the increased incidence of attacks received by victims, although contestants might also be preoccupied with monitoring their former opponents in order to assess whether a conciliatory initiative might be possible and/or indicate their own interest; in free-ranging Japanese macaques glances toward former adversaries have been found to be elevated following aggressive disputes and reduced again after reconciliation occurred (Koyama 1997). An explanation in terms of vigilance requirements is also suggested by the fact that longtailed macaque victims exhibit a post-conflict reduction in time spent foraging for small and dispersed items such as insects, but not in time spent eating from clumped food sources - an activity in which it is easier to keep an eye on one's surroundings at the same time (Aureli 1992). Following conflicts, both aggressors and victims in fact displayed an increase in time spent in prolonged visual scans of their surroundings, although the increase did appear somewhat more pronounced in victims. As this measure indexes only one component of vigilance behaviour, a large part of which consists of brief glances toward conspecifics or the environment, it nevertheless remains possible that overall levels of post-conflict vigilance are greater in the recipients of aggression (just as subordinate individuals typically spend more time monitoring others or fearfully scanning their surroundings than do dominant group members: Keverne *et al.* 1978, Shively 1998).

Recent victims therefore appear to continue to incur ecological costs whilst aggressors do not, with greater locomotion increasing the former's energetic requirements, whilst a temporary suspension of feeding behaviour suggests that energy intake is simultaneously reduced (with the caveat that time spent feeding does not always reflect actual food intake). In contrast, former aggressors spent more time interacting socially in the aftermath of conflicts than under baseline conditions. This latter increase is somewhat harder to interpret, as it is not clear whether the interactions recorded were predominantly affiliative or agonistic, and understanding their significance would depend upon also knowing which party - the contestant or its social partner - had initiated the interaction.

*Object-oriented activities*

Immature subjects were more likely to gnaw or manipulate objects such as branches, leaf litter or pebbles under post-conflict conditions. These activities did not resemble the

motions used when handling objects during playful interactions, being small movements, performed in a particularly repetitive and distracted fashion, and not directed toward social partners. As these behaviours had no apparent relevance to the ongoing situation, they should perhaps be regarded as "displacement" activities in the traditional sense (Tinbergen 1952, Zeigler 1964, Maestripieri *et al.* 1992). Such behaviours are hypothesised to arise when an individual is in a state of motivational conflict, and it is possible that following aggressive confrontations individuals are torn between a tendency to reapproach their opponent (in order to reconcile) or other partners, whilst being wary due to the risk of receiving renewed or opportunistic aggression (whether from the partner or its associates). Juvenile rhesus also commonly "fidget" in the same manner when thwarted from what appears to be a desired goal, for example when their play attempts are repeatedly rebuffed by an unwilling or sleepy recipient (personal observation). Similar activities have also been noted in adults in this population (e.g. soil-sweeping: Phillips 1998) and in other species; Kummer *et al.* (1974) describe how male hamadryas baboons "redirect grooming" to stones and other small objects, when they are attracted to a male-female pair yet simultaneously socially inhibited from interacting with the female. Common to all these situations is an impression of frustration on the part of the actor, which often seems motivated to initiate interaction with another individual under circumstances which may provoke a refusal, or even aggression from the intended partner or its close associates. Equally, it is also possible that these object-oriented behaviours are simply indicative of a physiological state of arousal rather than a specific state of motivational ambivalence, as has been proposed for other behaviours regarded as displacement activities and exhibited in the wake of aggressive encounters, such as self-scratching and autogrooming (Maestripieri *et al.* 1992; see next section). If so, this might explain why both former aggressors and victims displayed a post-conflict increase in object-oriented activities, given that the sympathetic activation produced by conflicts extends to both contestants.

Furthermore, the performance of such motor patterns in the aftermath of aggression could conceivably have a stress-relieving effect. Similar explanations have been advanced to account for displacement activities in general (e.g. Tinbergen 1952, Maestripieri *et al.* 92) as well as certain stereotypies (see review by Mason 1991). These have been interpreted as "coping responses" or re-regulating activities in situations of frustration or stress, which lower arousal and physiological responses to stress, and in some way keep the animal within optimal physiological and psychological limits. Unfortunately, as many of the studies exploring this possibility have been correlational in nature it has been difficult to ascertain whether the performance of these behaviour patterns was directly responsible for any associated physiological changes. However, a good example is provided by experimental work on laboratory rats, which demonstrated that those routinely allowed an outlet (such as gnawing on a piece of wood, or the opportunity to behave aggressively

toward conspecifics) when subjected to unavoidable physical stressors exhibited a diminished physiological response (measured in terms of glucocorticoid secretion) in comparison to others which were not given any opportunity to perform such behaviour (Levine *et al.* 1989). In the case of the particular activities reported here, it is possible that their rhythmic and repetitive nature might additionally have relaxing properties - akin to the use of worry beads in humans. This has already been suggested as a potential benefit of the stone-handling behaviour exhibited by free-ranging Japanese macaques (Huffman 1996), albeit in non-conflict situations. This necessarily remains speculative, as the physiological correlates of object-handling behaviour do not appear to have been investigated in nonhuman primates.

Manipulatory responses such as these do not seem to have been reported in previous studies of post-conflict behaviour - which typically use mixed-age subject samples - perhaps because object-oriented behaviour is primarily characteristic of young animals. Within a few weeks of birth, infant macaques typically investigate objects orally, exploration which is increasingly replaced by manual manipulation as infancy progresses. In many mammalian species the structure of play also follows an age-related pattern, with object- and locomotor-play predominating in early life (infancy), only later being replaced by increasingly social play (Baldwin 1986, Chalmers 1980). In general, juvenile animals appear more outwardly oriented, exploratory and neophilic than mature animals, no doubt as a consequence of the benefits of such behaviour in enhancing learning about the physical and ecological environment. For example, juveniles are more investigative and show lower latencies to approach novel objects and unfamiliar conspecifics than adults in both New and Old World taxa (e.g. Fairbanks 1993b, Mayeaux & Mason 1998). While adult macaques do occasionally handle natural objects such as rocks and sticks in a non-foraging context (e.g. Huffman 1984), immatures are much more likely to spontaneously manipulate such items (Menzel 1966, Huffman 1996; see Byrne & Suomi 1996 for similar age-related patterns of interest in both familiar and novel objects among tool-using species such as capuchins). Interestingly, Menzel (1966) reported that in free-ranging Japanese macaques spontaneous reactions to everyday objects were most frequent in 1-2 year olds and began to decrease sharply at 3-4 years of age; precisely corresponding to the age range studied here. Thus it would not be surprising if a predisposition toward object use in juveniles results in the manifestation of their displacement activities also being rather more object-oriented than those of adults.

*Behavioural indicators of tension*

Following conflicts subjects also exhibited a clear elevation in rates of self-scratching, which gradually declined toward baseline levels over the next ten minutes. Time budget data similarly showed that the proportion of time spent in either scratching or three other

self-directed activities (autogrooming, bodyshake and yawning) increased significantly in the aftermath of aggression. This is a common finding in primates; increases in a number of self-maintenance activities have been documented in situations which are generally stressful (e.g. Rowell & Hinde 1963, Troisi & Schino 1987, Pavani *et al.* 1991) and specifically in the post-conflict context (de Waal & Yoshihara 1983, Aureli *et al.* 1989, Aureli & van Schaik 1991b, Castles & Whiten 1998b, Das *et al.* 1998). Although focal animals exhibited an increase in scratching irrespective of their role in the preceding dispute, it was both more pronounced and longer-lasting in former victims and bidirectional participants, with subjects scratching at significantly lower rates following those incidents in which they had instigated hostilities. To some extent these patterns of self-directed behaviour may simply reflect arousal due to the exertions of the conflict and the physiological stress response evoked by the encounter. Following staged contests, in many species circulating levels of catecholamines and corticosteroids increase in both protagonists but are higher in the winner than in the loser, a disparity which is not merely the result of differential physical activity and which may persist for a period of hours (Brain 1980, Haemisch 1990, Sapolsky 1993, von Holst 1998). Similarly, both opponents exhibit evidence of sympathetic activation such as elevated heart rate and blood pressure after termination of an aggressive interaction, but heart rate returns to baseline levels more rapidly in the former aggressor (Smith *et al.* 1986, cited in Aureli & Smucny, in press; Smucny *et al.* 1997).

However the fact that reconciliation between former opponents causes both rates of scratching (e.g. Aureli *et al.* 1989, Aureli & van Schaik 1991b, Castles & Whiten 1998b) and heart rate (Smucny *et al.* 1997) to decline more rapidly in the wake of aggression, whilst affiliative contact with other individuals has a lesser or no effect (Das *et al.* 1998, Aureli & Smucny, in press), suggests that there may be more to the issue. There is evidence, albeit indirect, that self-directed behaviour is associated with circumstances producing emotional states of ambivalence and anxiety (Maestripieri *et al.* 1992; see introduction for additional details). Thus it has been suggested that motivational conflict over whether to approach a former adversary or to withdraw, and uncertainty regarding the future actions of others - specifically the risk of receiving aggression in the near future - contributes to the increased incidence of self-scratching seen under post-conflict conditions (Aureli *et al.* 1989, Aureli & van Schaik 1991b). Reconciliation, which is associated with a reduction in the rate of renewed or opportunistic attacks and a return to baseline levels of tolerance between the individuals concerned (Aureli & van Schaik 1991b, Cords 1992, Silk *et al.* 1996, Castles & Whiten 1998b), removes the presumed cause of any uncertainty. Again, the factors prompting such anxieties are more applicable to the victim of aggression than to the perpetrator. In despotic species such as rhesus the victim is usually the more subordinate party, and while the latter should have the most to gain if reconciliation is achieved this has to be weighed against the risk that a friendly

overture provokes a hostile response from its former assailant. Additionally, recent victims tend to be subject to increased rates of attack from third parties, whilst former aggressors do not (see section above). Furthermore, the magnitude of any anxiety experienced is likely to be influenced by the subject's perception of the event and of its current social position. In this species, victims do not possess the degree of control over the post-conflict situation enjoyed by aggressors (in terms of whether hostilities continue or not, whether reconciliation is granted or not), and perceived lack of control is known to be a very powerful variable magnifying the physiological effects of a stressor (Davis & Levine 1982, Sapolsky 1998).

Yet this hypothesis cannot really explain why former aggressors exhibit some increase in levels of scratching or self-grooming following conflicts (de Waal & Yoshihara 1983, Aureli 1997, Das *et al.* 1998, Castles & Whiten 1998b), despite not being at enhanced risk of receiving aggression, and even in species possessing a relatively strict dominance hierarchy in which such contestants should have little reason to be fearful of approaching their former targets; nor why reconciliation should be effective in reducing the occurrence of these self-maintenance activities in aggressors (e.g. Das *et al.* 1998; although see Castles & Whiten 1998b). These findings have recently been interpreted as perhaps indicating a more general form of anxiety concerning the state of the subject's relationship with a former adversary, for example whether it should expect tolerance and can continue to rely upon the other's cooperation (e.g. agonistic support) in the future, rather than simply uncertainty regarding the possibility of receiving aggression (Aureli 1997, Das *et al.* 1998). It is reasonable to expect that the benefits derived from and value attached to a peaceable relationship are asymmetric (cf. Cords & Aureli, in press), such that in despotic species in which aggressors tend to be dominant to their targets it is likely to be the subordinate party (i.e. the victim) which experiences greater anxiety of this form.

*Anxiety as an intervening variable mediating reconciliation*

If these emotional responses constitute a mechanism motivating recent opponents to initiate conciliatory overtures (Aureli 1997, Aureli & Smucny, in press), variation in the level of post-conflict anxiety experienced - here indexed by the rate of scratching - might be expected to parallel observed differences in reconciliation frequencies. However, the current study provides only partial support for such an assertion. One factor which is often associated with variation in conciliatory tendency is the context of the original dispute - fights over food are typically reconciled at lower rates than those with no obvious cause (chapter 3; de Waal 1984, Aureli 1992, Koyama 1997, Castles & Whiten 1998a). Immature subjects did in fact scratch significantly less often following the former type of conflict, a result which has been predicted but not found in previous studies (e.g. Castles & Whiten 1998b). One might argue that rates of both self-directed

and conciliatory behaviour might be lower in this context simply because the contestant is preoccupied with consuming the disputed resource, the latter being incompatible with the former activities. However this would seem unlikely where self-scratching is concerned; subjects were often observed to scratch themselves (e.g. with the hindlimbs) whilst already engaged in activities such as feeding or socializing, which tend to occupy both one's hands and one's attention. Additionally, such an explanation would be less applicable to the victim of aggression, which was often prevented from gaining access to, or was forced to relinquish, the resource at stake.

It therefore remains possible that differences in anxiety (or indeed, arousal) might be responsible for the variation observed. The lower rate of scratching following food conflicts did not appear to be merely a function of a lesser level of arousal being provoked by these conflicts. Disputes over food have sometimes been found to be of relatively low intensity (e.g. Koyama 1997, in free-ranging provisioned Japanese macaques), but in this study the two types of aggressive incident did not differ systematically in intensity, nor did the severity of the conflict influence the rate of subsequent scratching. Differential risk of resuming hostilities or receiving aggression from bystanders also could not have been the cause of a difference in anxiety, and hence in the scratching rates recorded, because conflicts over food were no less likely to be followed by subsequent attacks against the subject. Instead, a plausible explanation is that individuals' expectations influenced their perception of both the aggressive event and their social position, with conflicts over physical resources somehow producing less anxiety. A possible reason concerns the predictability of such conflicts. Subordinate individuals may learn through experience to expect threats or attacks when they are in possession of a material resource or if they approach a dominant while it is consuming food; such aggression may be stressful, but it is both predictable and understandable. Indeed, in species characterised by steep dominance hierarchies and low levels of tolerance, low-ranking individuals may be unwilling to approach desirable resources at all, when in the presence of a dominant animal (Diezinger & Anderson 1986, pers. obs.; see also experimental demonstration by Schaub 1995, in longtailed macaques). In contrast, conflicts which arise "out of the blue" can be neither anticipated nor linked to a specific cause, and therefore may cause the recipient to feel more anxious about its social position (for a similar argument regarding the likely efficacy of punishment which is applied unpredictably, see Miller 1997). In support of this, an extensive body of research on rodents and primates attests to the fact that a stressor which is applied unpredictably is more challenging physiologically (over time producing an increase in basal cortisol levels and a blunted glucocorticoid response to acute stress), than exactly the same stressor applied at regular intervals (e.g. Davis & Levine 1982, reviewed in Sapolsky 1998; see also Wingfield & Ramenofsky 1997). Clearly, this argument is less applicable to the perpetrators of aggression. Even in these individuals, though, it is

possible that conflicts over food simply are not as socially disruptive (Aureli 1992); dominance relations are "about" access to resources, thus in the aggressor's view a subordinate's continued presence near the resource may merit "punishment" because the dominant's expected priority of access has been contravened. Furthermore, if lower levels of anxiety in the recipient following aggression over food mean that the latter's behaviour (e.g. avoidance) also changes less than it would do otherwise, then former aggressors should have less cause for concern regarding future cooperation by, and potential damage to relationships with, their targets.

Another factor commonly found to affect conciliatory tendency is the quality of the relationship between protagonists, with conflicts between partners regarded as more valuable being reconciled more frequently (Kappeler & van Schaik 1992, Cords & Thurnheer 1993, de Waal & Aureli 1997; see chapter 3). If some component of a contestant's post-conflict anxiety is due to concern about possible disturbance to its relationship with the adversary (Aureli 1997, Das *et al.* 1998), then the greater loss of benefits commensurate with the demise of a more valuable relationship should induce greater anxiety following conflicts with these partners, and this may prompt such individuals to reconcile more frequently. Supporting this notion was the finding that longtailed macaque victims scratched at significantly higher rates when subjected to aggression from a close associate as opposed to a less affiliated individual (Aureli 1997). This result was not due to any systematic difference between conflicts with the two classes of opponent in either the intensity of the acts used, or in the risk of receiving further aggression. However, in the current study immature subjects did not scratch more following disputes with closely affiliated group members than after those involving less frequent associates, either when former aggressors or when victims. Nevertheless, these same subjects did reconcile more with close as opposed to other associates (chapter 3). Of course, one cannot rule out the possibility that the rate of self-scratching failed to fully reflect an underlying difference in anxiety. Yet if one presumes that scratching is as valid an index of emotion in immatures, the results suggest that some other factor must have been responsible for the observed difference in conciliatory tendency. A likely candidate is the greater degree of compatibility between group members which have a history of positive interaction; perhaps the relaxation of this constraint upon rapprochement following conflicts with certain types of partner, rather than a greater degree of anxiety, mediates the increased incidence of friendly reunions. After all, this proximate constraint has been proposed as an important determinant of reconciliation frequencies among immature individuals (Cords & Aureli 1993), and appears a plausible explanation for several of the patterns of conciliatory tendency documented in the previous chapter.

This leaves open the question of why conflicts within relationships presumed to be more valuable apparently were not associated with greater levels of anxiety, at least as indexed

by self-scratching behaviour. It is possible that the difference could be due to the age distribution of subjects used; perhaps the youngest immatures respond differently to aggression - for example *all* conflicts (outside the feeding context) might provoke appreciable anxiety. Yet there was no indication that the direction and magnitude of the difference in rates of scratching following the two types of conflict varied systematically with age, nor of the expected pattern being present in the oldest (subadult) cohort of subjects. It is also unlikely that juveniles do not discriminate between partners in terms of value; on the contrary, young individuals develop strong attachment to particular figures and react very strongly to temporary separation from those individuals (e.g. parents: Laudenslager *et al.* 1990, Dettling *et al.* 1998). Furthermore, the relatively small size of juvenile cercopithecines renders them particularly reliant upon agonistic support from older individuals, both in terms of protection from intragroup aggression and in gaining access to resources, and it seems unlikely that these allies would not be regarded as valuable. Although close associates are not necessarily also particularly valued partners (Cords & Aureli, in press), the conflation of these two factors cannot in itself explain the disparity in results between this study and that of Aureli (1997), as both measured "friendship" rather than partner value *per se*. However, it is possible that in immatures (but not in adults) there is a mismatch between the social partners with which an individual reconciles the most (i.e. close associates) and those which it finds the most valuable. As already discussed in chapter 3, the group members which a young subject may prefer as partners need not reciprocate this assessment; juveniles are usually not in a position to provide effective agonistic support or other benefits to older animals, especially in comparison with those available from other, more mature, partners who may therefore be rated more highly (cf. market effects, Noë & Hammerstein 1995). An illustration of this asymmetry is provided by work on grooming among female wedge-capped capuchins (O'Brien 1993); while juveniles directed their grooming toward adults, these individuals were more likely to terminate grooming sessions than were their young partners and often failed to reciprocate the grooming received, instead concentrating their attentions upon other adults. If older group members are unlikely to initiate post-conflict reunions with immature subjects, the latter may only be able to achieve high reconciliation rates with a subset of the partners which they value - those with which they happen to be familiar, and hence compatible. If variation in partner value does not closely parallel the division between close and other associates, we would not expect a consistent difference in anxiety levels following conflicts with "friends" as opposed to "others". Yet such an explanation ignores the fact that a partner's value derives not only from the level of benefits it can provide but also from its availability and tendency to act in such a manner (Kummer 1978); thus close associates may be the most valuable partners, whilst potentially useful group members which rarely reciprocate favours may not. Therefore it is worth considering the alternative possibility that, at least in this sample, the observed post-conflict increase in rates of scratching was due only to physiological arousal

combined with uncertainty regarding the risk of receiving further aggression, rather than being precipitated by concern about one's wider relationship with an opponent and hence influenced by the value attached to that relationship.

# 5

## *Post-conflict affiliation with third parties*

### *Introduction*

In many primate species, involvement in aggressive disputes - and therefore the attendant physical and social consequences - often generalizes to include individuals other than the original adversaries. Group members frequently intervene to aggressively support or defend one or other side in an ongoing confrontation (reviewed by Harcourt & de Waal 1992, Chapais 1995), and although such coalitions are known to occur in several avian and mammalian taxa (e.g. Russell 1983, Schilder 1990, Connor *et al.* 1992, Zabel *et al.* 1992, Marler 1996) primates are unusual in that multipartite involvement in intragroup aggression is commonplace (Harcourt 1988, 1992, Tomasello & Call 1996). Individuals may also "arbitrate" disputes by interposing and thereby terminating conflicts between other group members, or aggressively break up an interaction without siding preferentially with either combatant (e.g. Bernstein & Sharpe 1966, Boehm 1994; for recent theoretical treatment see Dugatkin 1998a). In a few species, bystanders even adopt a positive role by affiliating with or appeasing a contestant during an ongoing dispute (e.g. Petit & Thierry 1994a), which has been interpreted as a diverting tactic to terminate aggression against the recipient's adversary without simultaneously coming into conflict with the recipient itself. Bystanders are also likely to become embroiled in aggression after the initial confrontation has subsided. Redirection of aggression, whereby former victims initiate attacks against previously uninvolved third parties is a common response to aggression in many taxa, but has been particularly noted in several cercopithecine species (Scucchi *et al.* 1988; see chapter 6 and references therein). For their part, macaque bystanders also exhibit a tendency to opportunistically attack the victims of recent aggression (Aureli & van Schaik 1991b, Castles & Whiten 1998b; see also chapter 4), perhaps because this situation affords a relatively safe way to gain an advantage over the target. Subsequent outbreaks of aggression, in which the relatives of two parties which have recently fought later retaliate against each other, have also been reported to occur ("vendetta": Cheney & Seyfarth 1986, Aureli *et al.* 1992).

Given this potential for bystanders to become entangled in aggression originally instigated by others, it would seem likely that group members possess an interest not only in monitoring and influencing the course of others' conflicts, but also might seek to influence post-conflict events via peaceful means, to their own or their allies' advantage. Furthermore, the combatants themselves might seek affiliation with previously uninvolved third parties, as a calming interaction and/or a means of protection from further attacks. Post-conflict affinitive exchanges between contestants and bystanders have in fact been documented in a variety of primate species (e.g. Judge 1991, de Waal

& Aureli 1996, Das *et al.* 1997 and references therein), variously being termed "consolation", "substitute reconciliation" or "triadic affiliation", depending upon the identities and direction of initiative of the parties involved; in the majority of studies the focus has been upon bystanders related to the original contestants. This chapter instead uses the general label "third party affiliation" (TPA), additionally specifying the subset of third party partners involved where appropriate.

For example, several studies have documented an increase in affiliation between conflict participants and their own relatives under post-conflict conditions (e.g. Cheney & Seyfarth 1989, Judge 1991, Petit & Thierry 1994c), over and above their already high baseline rates. In many cercopithecines maternal kin are favoured proximity, co-feeding and contact partners (reviewed in Gouzoules & Gouzoules 1987), often engaging in affiliation at high rates even when interaction frequencies are corrected for the greater time spent in proximity (Kurland 1977, Berman 1982). This may be combined with relatively low rates of aggression, at least when their greater time in association has been taken into account (e.g. Bernstein *et al.* 1993; see also de Waal 1993b concerning selective tolerance of close relatives around critical resources). Thus we might expect that if former combatants seek calming contact with others when aroused or distressed, their close relatives would be the most familiar and "safe" alternatives. Furthermore, close kin are also the group members most likely to aggressively intervene on one's behalf during conflicts (e.g. Kurland 1977, Kaplan 1978, Bernstein & Ehardt 1985a, Netto & van Hooff 1986), often providing high rates of support even when their greater social and spatial availability have been taken into account. Therefore, it is possible that by maintaining proximity to likely supporters following conflicts, former contestants reduce the chances of receiving retaliatory or opportunistic attacks from previous opponents or other group members. Finally, due to their indirect fitness interests, related bystanders are likely to be the individuals most motivated to act in ways which would ameliorate the stressful effects of contests upon a groupmate, and to approach to provide protection if needed. It is not clear to what extent such behaviour would require an understanding of the recipient's distress, and hence whether or not the cognitive capacity for empathy (which monkeys appear to lack; de Waal & Aureli 1996) would be necessary.

However, affiliative exchanges which take place with a contestant's own relatives in the wake of a conflict are unlikely to entirely alleviate the presumed cause of any anxiety and increased risk of aggression, namely its uncertainty regarding the future actions of, and potential damage to the relationship with, its former adversary. Post-conflict affiliation with maternal kin of the opponent has been documented in several studies (e.g. Judge 1991, Das *et al.* 1997, Castles & Whiten 1998a) and it has been suggested that bystanders may thereby reconcile "on behalf of" their relative (Cheney & Seyfarth 1989, Judge 1991), whilst contestants may use such contact as a "substitute" for direct

reconciliation with the opponent in situations where the latter is difficult to achieve (Aureli & van Schaik 1991a). It is not clear how such a change in the disposition and future behaviour of the opponent could be brought about, although it is possible that these interactions are merely an indirect route to contact with the opponent itself, increasing the chances that they will eventually meet by bringing the two kin cliques into proximity. More simply, it is possible that these exchanges are appeasing, initiated in order to prevent aggression spreading to involve further members of the matriline (Judge 1991). After all, close kin of former opponents have been suggested to be disproportionately implicated in the spread of subsequent aggression, either being the targets of redirected attacks or involved in subsequent retaliation (Cheney & Seyfarth 1986, 1989, Aureli *et al.* 1992; see also chapter 6). Therefore it is possible that both the contestant and its opponent's relatives may have reason to try to preempt such attacks.

Little is known about post-conflict interactions between immature contestants and third parties, and current evidence is contradictory. It is possible that these conflict management strategies are particularly prevalent among young individuals. For example, the relatively small size and on average low rank of immature group members puts them at a disadvantage, thus they may be at greater risk than adult contestants of receiving subsequent attacks from opportunistic bystanders or powerful supporters of the former opponent, and may need to move to preempt this threat. As youngsters are likely to be used to experiencing protection from mothers or older relatives they might be expected to seek proximity to such individuals after conflicts, as reported by Pereira (1993) and Watts (1995b). Furthermore, because juveniles are often the recipients of aggression from older conspecifics (e.g. Bernstein & Ehardt 1985c, Pereira 1988b), in these cases the victim may be inhibited from approaching a much more powerful opponent directly, and may instead seek to affiliate with the latter's younger and more approachable kin if available, as has been suggested by Aureli & van Schaik (1991a). The latter authors could not demonstrate a post-conflict increase in affiliation between victims and the former aggressor's kin in their entire age sample of captive longtailed macaques, but an effect was demonstrable when immature victims were considered alone. This tactic might therefore be most useful to the youngest juveniles, and should be most frequent following conflicts where the age (and hence size) differential between participants is relatively great. In contrast, Judge *et al.* (1997) apparently found no evidence for third party post-conflict affiliation of any kind in captive juvenile rhesus macaques. In a similar vein, Cheney & Seyfarth (1986) documented the occurrence of both "simple" (versus a relative of one's opponent) and "complex" (between the two sets of relatives, rather than involving the protagonists themselves) kin-oriented redirected aggression in mature wild vervets, but only a nonsignificant trend towards simple redirection and no evidence for the complex form in individuals under three years of age, results which they speculated might be due to a lack of relevant knowledge about third party relationships in

immatures. This would suggest that post-conflict affiliation between juvenile contestants and kin of their former opponents is unlikely to occur unless initiated by an older bystander.

The primary aim of this chapter is therefore to examine whether affiliative interactions between immature contestants and bystanders occur in the wake of aggressive confrontations, focusing specifically upon third parties related to one or other of the original opponents. As a post-conflict increase in contacts with a particular bystander class might simply be due to a generalized increase in affiliation with all group members, it is naturally important to additionally demonstrate that any increase observed is specific to the partner type of interest. Whilst some form of "selectivity" test (de Waal & Yoshihara 1983) is almost invariably presented in studies examining the friendly reunions which take place between former opponents, authors have been rather less consistent in checking whether post-conflict affiliation with specified bystander classes is also disproportionately enhanced (Das *et al.* 1997). For this reason, the possibility of a post-conflict increase in affiliation with a "comparison group" of third party partners - individuals unrelated to either of the contestants - has also been examined and the magnitude of any elevation in affiliation with the bystander class of interest assessed relative to that seen with this nonkin category.

Two further issues have also been given special attention. Firstly, male and female subjects might be expected to differ in the extent to which post-conflict interactions take place with bystanders on the basis of their relatedness to (or more strictly, their close association with) the former adversaries. In general, female macaques exhibit a greater bias toward matrilineal kin in their affiliative interactions than do males, presumably as a consequence of female natal philopatry and hence the fact that females have much greater opportunity to form lifelong bonds with maternal relatives (see chapter 3 for further discussion of this point). These differences between males and females in the overall importance of kin bonds, which are apparent from an early age, are likely to be reflected in similar sex differences in post-conflict affiliative behaviour. Secondly, the subject's role in the original conflict (i.e. whether aggressor or victim) has been distinguished in analyses, as in a number of prior studies of cercopithecines TPA has either failed to be demonstrated in former victims (e.g. Cords 1988, Aureli & van Schaik 1991a, Judge 1991) or a significant *reduction* in affiliation involving victims is exhibited under post-conflict conditions (e.g. Aureli *et al.* 1993, 1994). These negative results have been suggested to be due in part to the constraints of a strict dominance hierarchy in many macaque taxa, which may make it risky for bystanders to associate with the recipients of aggression even if they wish to do so (Aureli *et al.* 1994) . However, given that contact between prior victims and bystanders appears common in the aftermath of conflicts between chimpanzees but is rarely documented in macaques (de Waal & Aureli 1996), it

is also possible that the lack of a capacity for empathy in the latter reduces the tendency of bystanders to approach distressed former contestants in these species.

Finally, post-conflict affiliation directed preferentially toward a former opponent's relatives is also interesting from a cognitive standpoint, as it implies an understanding of the relations which hold between third parties - at least in those cases where the contestant initiated the interaction. Primates appear particularly adept at acquiring and using such social information (Tomasello & Call 1996), and experimental evidence suggests that adult and subadult papionines recognise both the kin bonds (Dasser 1988a,b, Cheney & Seyfarth 1999) and relative rank of other group members (Cheney *et al.* 1995a). Demonstrations of post-conflict increases in affiliation with relatives of former opponents and of kin-oriented redirection of aggression (see chapter 6), based upon observational data, have often been taken as evidence of the former ability (e.g. Cheney & Seyfarth 1986, 1989). Nevertheless, these patterns of behaviour need not require any such understanding on the part of the actor. Close kin tend to associate spatially in rhesus macaques (see references provided above) and in particular tend to cluster at the scene of aggression, with relatives of the protagonists often being attracted to the vicinity even if they do not subsequently intervene themselves (pers. obs.). If kin of participants are over-represented among the bystanders present, use of a simple behavioural rule - such as "contact a nearby individual" - could produce a disproportionate increase in affiliation between contestants and relatives of their former opponents, in the absence of any recognition or active selection of these individuals as partners (see Cords 1997 for a similar hypothesis). Before accepting an overly cognitive interpretation one should first check for simpler alternatives (for example see de Waal & Luttrell 1988 and Hemelrijk 1996 for an analagous discussion, regarding proximity- or symmetry-based explanations for apparently calculated reciprocity), as in nature comparatively simple algorithms may often suffice to produce apparently complex patterns of behaviour. Therefore any post-conflict increase in affiliation between immature combatants and the kin of former opponents will subsequently be examined to determine whether or not patterns of proximity at the time of the conflict could have accounted for the result obtained.

# *Methods*

## *Definitions*

*Subject role* Following the definitions provided in chapter 3, the *aggressor* was the individual which exhibited the first aggressive act of the conflict, whilst the recipient of this initial aggressive act was termed the *victim*. All analyses in which aggressors and victims are treated separately have been restricted to those PC/MC pairs in which the direction of aggression in the original conflict had been unambiguous; i.e. counter-aggression had not occurred.

*Subject age* Refers to the focal individual's cohort age, in years (see chapter 2).

*Bystander* This term refers to all group members not involved in the original dispute, therefore excluding the original initiator and recipient of aggression and, in polyadic conflicts, any simultaneous victims, helpers or aggressive supporters of either side.

*Kinship* Individuals were classified as *close kin* if they were related through the maternal line at, or more closely than, the level of cousins (degree of relatedness $r \geq 0.0625$; note that this value assumes no inbreeding or sharing of paternal genes). For further discussion of this definition, see chapter 3. All other individuals from the same matriline were termed *distant kin* ($0 < r < 0.0625$), whilst members of different lineages were regarded as *nonkin* ($r = 0$). In analyses, the subject's *own kin* and its *opponent's kin* refer to bystanders related at the *close kin* level to either the subject or its initial adversary, respectively. In cases where the original conflict had been between opponents from the same extended matriline a relative measure of kinship was used, such that a social partner was regarded as the subject's own kin if it was more closely related to the focal animal than to the latter's initial opponent, and as the opponent's kin if it was more closely related to the initial opponent than to the focal animal (see Judge 1991 for similar reasoning). PC/MC pairs in which the conflict had been between a mother-offspring dyad (in which, by definition, all other matriline members would be more closely related to the mother than to the offspring) or between maternal siblings (in which all social partners from the same matriline would be equally related to both opponents) therefore had to be excluded from analyses of TPA with own kin and opponent's kin partners.

*Post-conflict affiliation* Any clearly directed affiliative signal or interaction involving the focal immature was scored, including nonagonistic contact and gestures or vocalizations defined as affinitive in this species (further definitions are provided in chapter 3 and Appendix B). The gesture "present", which may be used to initiate affiliative interactions but is also used in submissive contexts (Maestripieri & Wallen 1997, Dixson 1998), was counted only if accompanied by other affiliative signals from at least one of the parties involved. Approaching to within proximity (defined as within arm's reach, ≤0.6m) was

not counted if unaccompanied by any affiliative signal. Following Das *et al.* 1997, the proportion of first affiliative interactions with each category of partner which involved actual physical contact within the initial bout has also been reported, to provide some comparison with previous studies which based analyses solely on interactions involving contact.

### *Data analysis*

Analyses were conducted upon 441 pairs of post-conflict (PC) and matched-control (MC) observations, collected on 108 focal immatures aged between 1 and 4 years. Further details concerning data collection and the distribution of these paired observations across age, sex and conflict role categories are provided in chapter 2. Not all PC/MC pairs were suitable for use in every analysis, and specific exclusions are outlined below.

I first examined whether tendencies to affiliate with two specific categories of previously uninvolved partners, the subject's own relatives and those of the initial opponent, were elevated under post-conflict conditions. All analyses are based upon a derivative of the PC-MC method (de Waal & Yoshihara 1983), in which the relative latency to the first affiliative action with a specific category of partner is assessed within pairs of PC and MC observations, and each PC/MC pair then designated as either "earlier", "later" or "neutral" (see chapter 2 for further explanation of both this procedure and the following methods). The first affiliative act was defined as the first to occur with any partner belonging to the class of individuals under consideration, per PC or MC sample. A Wilcoxon signed-ranks test was then utilised to determine whether the proportion of "earlier" pairs (EP) was significantly greater than that of "later" pairs (LP), at the individual level.

Matched pairs of PC and MC observations pertaining to conflicts in which the focal animal, or its initial opponent, did not possess any close relatives in the group at the time were excluded from analyses of affiliation with own kin, or opponent's kin, partners respectively. The 13 PC/MC pairs in which one observation had been truncated before 10 minutes were utilised only when the duration of the shorter sample exceeded the time period required by the analysis (being either 10 minutes, or a shorter time window), or if the first affiliative act with the partner category of interest had occurred in either the PC or MC observation before the latency at which the shorter sample terminated. Finally, in some observations, the subject was already engaged in an affinitive interaction with a third party at the point when the sample commenced. PC/MC pairs containing such samples were omitted from analyses concerning the class of partner to which the third party belonged, in order to avoid an artificial accumulation of contacts "established" at $t=0$. For example, if a subject was playing with its younger sibling at the start of an MC, this matched pair would be excluded from analyses concerning affiliation with own kin

bystanders, but could still contribute to those concerning affiliation with unrelated bystanders.

It is possible that basing the PC-MC comparison upon the entire (and arbitrary) 10-minute duration of PC/MC observations could lead to a post-conflict increase in affiliation being overlooked, in cases where the baseline level of affiliative interactions with a particular partner class is itself high and any post-conflict increase is limited to only the first few minutes following a conflict (Aureli *et al.* 1989, Veenema *et al.* 1994). The partner classes considered in this chapter are likely to exhibit high baseline levels of first interactions, due both to the large number of potential partners available in each class (applicable to all three bystander categories examined) and/or a high motivation to interact sociopositively with certain types of group member (e.g. maternal kin). Therefore I also checked for the existence and influence of any early PC increase by conducting tests using information from a shorter time-frame following the conflict. The duration of the appropriate time window (if any) was located by utilising a Kolmogorov-Smirnov two-sample test to examine whether the relative cumulative frequency distributions across time of first affiliative acts in the PCs and in the MCs differed significantly (time-rule method, Aureli *et al.* 1989). Only the first affiliative interaction with any member of the specified partner class was utilised, per observation. If significant, the time window was taken to be the latency (in 10 second intervals) at which, in the aggregate sample, the difference between the two relative cumulative frequency distributions was first maximal. For each category of social partner examined, the frequency distribution over time of first acts in post-conflict and in control samples has therefore been presented, and in each case the length of any applicable time window is specified. In order to check that the result obtained had not been due to the extreme behaviour of a few individuals, I also examined whether the proportion of PC observations containing at least one affiliative interaction with the partner class of interest within this initial time window was significantly greater than the equivalent proportion of MCs, at the individual level (cf. Aureli & van Schaik 1991a).

This analysis differs from several previous studies in that the time-rule was not used as a method of demonstrating whether a post-conflict increase in affiliation existed; instead, the original PC-MC comparison using individual scores was repeated upon data drawn only from the early time period identified as relevant by the time-rule, a procedure which has also recently been advocated by Das *et al.* (1997). Whenever such a second and only partially independent PC-MC test was performed an approximate - although rather conservative - correction factor was employed, by halving the significance criterion required for the second test (i.e. $p \leq 0.025$); cases where this more rigorous alpha level was not met are discussed separately in the text. Further discussion of both these points is provided in chapter 2.

Responsibility for initiating first interactions was also examined, the initiator being defined as the party which first approached to within arm's reach (≤0.6 m) or which directed the first affiliative signal (if not preceded by an approach), where an affiliative interaction between two individuals then occurred. As the pattern of initiative exhibited under post-conflict conditions should revert to that characteristic of baseline affiliation over time, in the PCs I focused upon those first acts which fell within the early window of elevated PC affiliation relevant to the partner category in question (see Aureli *et al.* 1989). In MC observations, the first act to occur at any point in the 10-minute period could be utilised.

I then investigated whether variables such as age, sex and role in the previous conflict influenced the degree to which post-conflict affiliation with particular classes of bystander was elevated above baseline levels of interaction. Comparisons between individuals were performed using Mann-Whitney *U* tests, and based upon individual scores of corrected affiliative tendency (AT). The latter measure, analagous to the corrected conciliatory tendency index devised by Veenema *et al.* (1994), allows potential variation between individuals in baseline levels of interaction to be taken into account when calculating the post-conflict incidence of a behaviour. Affiliative tendency for an individual with respect to a specific class of partner is defined as (E-L)/T, where E represents the number of "earlier" pairs, L the number of "later" pairs, and T the total number of eligible PC/MC pairs possessed. This measure is calculated per individual, irrespective of whether it was the focal subject or the social partner which initiated the first interaction.

Where a post-conflict increase in the likelihood of affinitive interaction between focal animals and a specific class of bystanders has been established, it is important to verify whether or not this result is merely due to a more general increase in such behaviour with all group members, rather than being selective to the partner category in question. Interactions with nonkin bystanders (i.e. all bystanders which did not belong to the matrilines of either the subject or its initial opponent) were used as a comparison group for this purpose; interactions with distant kin being excluded in order to create distinct and unambiguous categories of partner (see Judge 1991, and Das *et al.* 1997, for similar logic). After establishing whether affiliation with even this nonkin subset of group members was enhanced under post-conflict conditions, I examined whether the increase above baseline levels with respect to kin (or opponent's kin) partners was greater than any increase observed with nonkin partners. This was simply achieved by testing whether subjects' AT scores for the bystander class of interest were significantly greater than their AT scores with respect to nonkin bystanders. The affiliative tendency index was utilised in order to take into account potential differences between partner classes in baseline levels of affiliation, which may be expected to vary depending upon the differing numbers of individuals present in each class, their likelihood of meeting and their motivation to engage in affinitive interactions, among other factors. For similar

reasoning, and an alternative index of selectivity also based upon the relative latency to first acts in PC versus MC observations, see Das *et al.* (1997). Selectivity tests were first conducted using the full 10-minute observation period and, as with the basic PC-MC comparisons described above, if a comparison between subgroups proved nonsignificant the result was then checked by limiting the analysis to the initial time window of PC increase appropriate to the partner category of interest (i.e. own kin, or opponent's kin).

Two further checks were also conducted in the case of affiliation with the opponent's kin. As Das *et al.* (1997) have pointed out, it is possible that a post-conflict increase in affiliation with relatives of the former opponent might be merely a side-effect of reconciliation with the opponent itself, rather than being specifically directed toward the latter's relatives. If individuals tend to associate spatially with their kin under post-conflict conditions (as they do under baseline conditions), then proximity of the former contestants is likely to bring each into the vicinity of the other's relatives, thereby providing contestants and these bystanders with an increased opportunity to interact. To establish whether this was the case, PC/MC pairs in which any approach or overt affiliation between the subject and its initial opponent had taken place ***before*** or at the ***same time*** as the occurrence of any affiliation (or of any approach preceding that affiliation) with the initial opponent's kin, in either the PC or the MC, were excluded. The PC-MC comparison was then repeated within this subset of the data, to see whether a significant PC increase was still apparent.

Even so, it is possible that contestants and relatives of their opponents exhibit a selective increase in post-conflict affiliation, not because these partners select each other, but simply because the opponent's relatives are over-represented (e.g. relative to nonkin bystanders) among the individuals in proximity at the time. Thus a rule-of-thumb in which contestants simply affiliated with the nearest bystander might be sufficient to ensure that kin-biased triadic affiliation occurs, but would not necessarily imply that the subject recognises the association between its former adversary and particular third parties and then acts on that basis. Ideally, one would compare the proportion of individuals within proximity (defined as ≤5m radius of either participant) at the commencement of a PC observation which were related to the opponent, with that in the corresponding MC, and relate these measures to whether an "early" post-conflict interaction with the opponent's kin took place or not. Unfortunately, complete proximity data were not collected at the start of MC observations. Therefore, for each focal animal, the affiliative tendency (AT) with the opponent's kin in PC/MC pairs in which at least one member of the opponent's family had been within 5m at $t$=0 in the PC, was compared with that from pairs in which no relative of the opponent had been within proximity at the start of the PC. As an estimate of those in proximity at the moment the conflict terminated and the PC observation commenced, I used all individuals within ≤5m at the start of the conflict together with all individuals which had approached to within

≤5m of, or had been approached by, the contestants during the course of the conflict (excluding the opponents themselves and any helpers or supporters which took part). In some cases, this may have slightly overestimated the actual number of bystanders in proximity by the end of the conflict (for example if a prolonged chase took place). One should note that such a test may be overly harsh, in that even if representatives of the opponent's kin were present in close proximity, the family member with which affiliation actually took place may nevertheless not have been nearby at the start of the observation (and thus was truly "selected").

To retain maximum sample size, all analyses were initially conducted using scores derived from all individuals possessing eligible PC/MC pairs, with no criterion regarding the minimum amount of data per individual. Therefore, before concluding that no significant difference existed in a particular comparison, I also checked whether the apparent lack of an effect might simply be due to limitations in the accuracy of the individual scores being used. This was achieved by restricting the comparison to subjects possessing ≥3 usable PC/MC pairs for the analysis concerned (where a within-individual comparison was involved - e.g. between conflicts as a former aggressor or former victim - this criterion had to be relaxed to ≥2 eligible pairs, because individuals were required to attain the minimum number of pairs in *each* of the categories being compared).

All statistical analyses were conducted upon individual scores, and two-tailed tests were utilised throughout. The only exception concerned Kolmogorov-Smirnov tests used to estimate the time window of elevation of PC affiliation, which were based upon first events occurring in the aggregate sample of observations and, given that the direction of the expected difference (i.e. a PC increase) had already been ascertained using the PC-MC method, were by definition one-tailed. Ideally, multivariate statistics would allow simultaneous assessment of factors (such as subject age, sex, and role in previous conflict) potentially affecting affiliative tendencies with specific classes of partner. However in many cases the data did not satisfy all the assumptions of such procedures, and thus variables were examined independently using non-parametric tests. In each analysis $N$ refers to the number of individuals used, whilst the total number of PC/MC pairs contributing towards a particular test may be presented in parentheses or in the Figure legend. Values presented refer to the mean (± SE) of individual AT scores, unless otherwise specified. The significance level was set at 5% unless a correction factor was in force, and $p$-values of between 0.05 and 0.10 are referred to as nonsignificant trends or tendencies.

## *Results*

### *Affiliation with own kin*

Focal animals exhibited significantly earlier affinitive interactions with their own close relatives under post-conflict conditions (48.2% EP and 26.4% LP from a total of 334 PC/MC pairs; Wilcoxon: $N = 99$, $Z = -4.26$, $p = 0.000$). This result was not due to post-conflict affiliation taking place mainly between subjects and relatives which had supported them in preceding polyadic disputes, because the definition of "own kin" partners specifically excluded all individuals which had taken part in the original conflict. Nor was the observed post-conflict increase unduly influenced by 6 of the oldest female subjects which had given birth for the first time during the course of the study, and might have been expected to re-establish contact with a dependent infant soon after being involved in any confrontation; excluding these females did not affect the outcome of the above analysis. Mean affiliative tendency was 0.25 ($N = 99$ individuals), and first bouts typically involved body contact - of the 195 first interactions documented in the PCs, 88.2% included physical contact.

A Kolmogorov-Smirnov test revealed that the relative cumulative frequency distributions of first affiliative acts in PCs and in MCs were significantly different (Fig. 5.1; $m = 195$, $n = 153$, $X^2 = 20.47$, $df = 2$, $p < 0.001$, 1-tailed), the maximal difference being located at <110 seconds after the conflict. This time window was also representative of the behaviour of individuals, as the proportion of PCs in which the first affinitive interaction between a subject and its kin occurred within <110 seconds was significantly greater than the equivalent proportion of the same subject's MC observations, at the individual level (PC = 0.30 ± 0.03, MC = 0.13 ± 0.02; Wilcoxon: $N = 99$, $Z = -4.23$, $p = 0.000$). As illustrated in Figure 5.1, PC levels of first acts were substantially higher than MC levels immediately after conflicts, and rapidly declined to then mirror the MC distribution. The fact that even MC levels of first acts decline slightly over time is due both to a high probability that subjects will become involved in affiliation with at least one close relative at some point during the observation (for reasons see methods section), and a consequence of counting only the very first interaction with a member of that partner class - at later time intervals, fewer and fewer observations remain in which a first interaction has not already taken place and hence can be scored (see de Waal & Aureli 1996 for a similar phenomenon).

### *Subject attributes and role in previous conflict*

As the importance of maternal kin as affiliative partners may differ between male and female subjects, separate analyses were performed for these two subsets of individuals. Both sexes exhibited a significant post-conflict increase in affinitive interactions with own

kin partners (males: 43.8% EP and 26.1% LP; Wilcoxon: $N = 49$, $Z = -2.87$, $p = 0.004$; females: 53.1% EP and 26.6% LP; Wilcoxon: $N = 50$, $Z = -3.11$, $p = 0.002$). Nevertheless, the degree of post-conflict increase was significantly greater in immature females than in their male counterparts. Although a comparison between the sexes regarding affiliative tendency toward own kin partners was not significant when conducted over the full 10-minute observation period ($AT_{male} = 0.21 \pm 0.07$, $AT_{fem} = 0.29 \pm 0.08$; Mann-Whitney: $m = 49$, $n = 50$, $Z_{corr} = -1.03$, $p = 0.304$, NS), a significant difference emerged when this result was checked using the relevant initial time-frame of <110 seconds and the more accurate scores of individuals possessing a minimum of 3 PC/MC pairs ($AT_{male} = 0.21 \pm 0.08$, $AT_{fem} = 0.27 \pm 0.08$; Mann-Whitney: $m = 29$, $n = 25$, $Z_{corr} = -2.44$, $p = 0.015$). Nevertheless, given that both sexes had exhibited a significant PC increase in such affiliation, males and females were combined in the following two analyses, in order to retain maximum sample size.

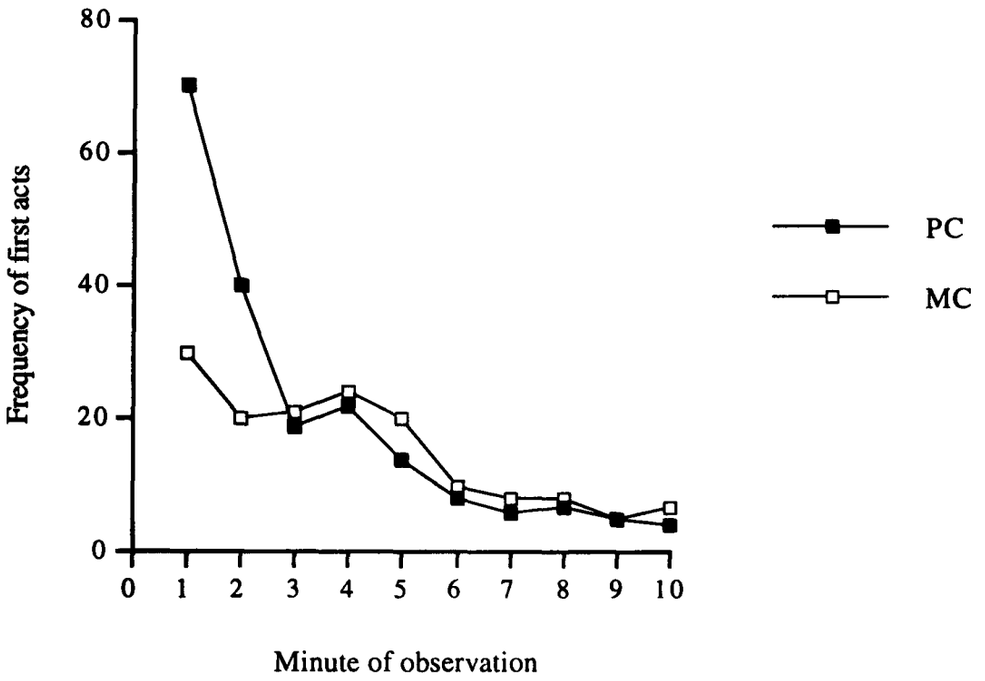



*Figure 5.1.* Distribution over time of first affiliative interactions with related bystanders in aggregate post-conflict (PC) versus matched-control (MC) observations. For each observation, only the first interaction between the subject and an individual from this partner class has been taken into account. Although the Kolmogorov-Smirnov test utilised 10-sec intervals, for simplicity results have been summarised using 1-min intervals in this and subsequent figures. From 334 PC/MC pairs.

The age of focal subjects did not appear to influence their tendency to affiliate with, or receive positive overtures from, closely related bystanders. No significant correlation existed between individual AT scores with respect to own kin partners and age cohort in years (Spearman: $N = 99$, $r_s = -0.07$, $p = 0.516$, NS). This result remained

nonsignificant when the comparison was restricted to the initial <110 second time window, and limited to individuals possessing 3 or more eligible PC/MC pairs.

PC/MC pairs following conflicts in which aggression had been uni-directional were used to examine whether both former aggressors and former victims were involved in post-conflict affiliation with related bystanders. Former aggressors exhibited significantly earlier affinitive interactions with own kin partners in PC observations, even when the entire 10-minute time-frame was considered (49.1% EP and 24.1% LP; Wilcoxon: $N$ = 58, $Z$ = -2.37, $p$ = 0.018). Former victims did not exhibit this pattern when the full 10-minute observation period was examined (44.9% EP and 32.0% LP; Wilcoxon: $N$ = 76, $Z$ = -1.32, $p$ = 0.186, NS), although PC interactions were found to occur earlier when the comparison was limited to the initial <110 second time window (29.5% EP and 14.8% LP in first 110 sec; Wilcoxon: $N$ = 77, $Z$ = -2.09, $p$ = 0.036). This latter result requires further confirmation, however, as the preferred significance criterion of $p \leq 0.025$ was not achieved in this test (see chapter 2). For individuals which possessed PC/MC pairs in both roles, there was some indication that a subject's role in the preceding conflict affected the likelihood that it would be involved in post-conflict affiliation with related third parties. There was a nonsignificant trend for higher affiliative tendencies with own kin bystanders following conflicts in which the focal animal had been the instigator of aggression rather than its recipient ($AT_{aggr}$ = 0.31 ± 0.10, $AT_{vict}$ = -0.02 ± 0.12; Wilcoxon: $N$ = 42, $Z$ = -1.80, $p$ = 0.073, NS) but this effect was no longer present when the test was conducted within the initial <110 second time-frame ($AT_{aggr}$ = 0.25 ± 0.06, $AT_{vict}$ = 0.09 ± 0.09; Wilcoxon: $N$ = 43, $Z$ = -1.22, $p$ = 0.224, NS). The comparison remained nonsignificant when restricted to the handful of individuals which possessed two or more eligible pairs in both roles. In combination the above results suggest that the post-conflict increase in affiliation with own kin bystanders is somewhat less pronounced after conflicts in which the subject had been the former victim rather than the aggressor, although the difference between the two roles is not significant.

*Initiative*

To investigate whether the former combatant or its relative tended to establish affiliative interactions, and whether the responsibility for initiation differed according to the focal animal's role in the prior conflict, first acts occurring within the <110 second window in PCs were examined. Of 105 such first acts in the PCs, the majority (65.7%) were instigated by the immature contestant. This was very similar to the pattern of initiative exhibited in the MCs, where all 153 first acts occurring at any point in the 10-minute observation could be utilised - 62.1% being initiated by the young contestant. Post-conflict initiative did not differ appreciably according to a subject's role in the preceding

dispute; following unidirectional conflicts in which the subject had been the aggressor 64.9% of 37 first acts were initiated by the contestant, and following those in which the subject had been the victim 68.8% of 48 first acts were instigated by the contestant. In all 3 cases, very similar figures were obtained if the sample of first acts was increased by utilising all 195 first acts occurring at any point in the 10-minute duration of the PCs.

### *Affiliation with the opponent's kin*

Focal animals also engaged in significantly earlier affinitive interactions with close relatives of their initial opponent in post-conflict than in matched-control observations (24.1% EP and 7.5% LP of 320 PC/MC pairs; Wilcoxon: $N = 102$, $Z = -3.67$, $p = 0.000$). It should be noted that as the definition of the partner category "opponent's relatives" specifically excluded all individuals which had been supporters or helpers in the original conflict, this result was not due to focal animals merely affiliating with secondary opponents. Mean individual affiliative tendency was 0.17 ($N = 102$ individuals), and 71.8% of the 78 first bouts of affiliation which occurred in PCs involved actual physical contact.

The relative cumulative frequency distributions across time of first acts in the PCs and in the MCs differed significantly (Kolmogorov-Smirnov: $m = 78$, $n = 38$, $X^2 = 6.41$, $df = 2$, $p < 0.05$, 1-tailed), with the maximal difference between the two distributions again being located at <110 seconds. A comparison of the proportion of each individual's PC versus MC observations which contained an affinitive interaction with a close relative of the former opponent within the first 110 seconds confirmed that the duration of this time window derived from the aggregate sample had not merely been due to the extreme behaviour of a few subjects (PC = 0.12 ± 0.02; MC = 0.03 ± 0.01; Wilcoxon: $N = 102$, $Z = -2.94$, $p = 0.003$). Figure 5.2. illustrates the frequency distribution over time of first affiliative interactions with bystanders which were closely related to the subject's initial opponent.

### *Subject attributes and role in previous conflict*

Given the differing importance of kin bonds for male and female macaques, the PC-MC comparison was again performed separately for male and female subjects. Both males and females exhibited significantly earlier affinitive interactions with close relatives of their former opponents under post-conflict conditions (males: 21.1% EP versus 6.2% LP; Wilcoxon: $N = 50$, $Z = -2.70$, $p = 0.007$; females: 27.0% EP versus 8.8% LP; $N = 52$, $Z = -2.48$, $p = 0.013$). Furthermore, the sexes did not differ significantly in affiliative tendency ($AT_{male} = 0.16 \pm 0.05$, $AT_{fem} = 0.18 \pm 0.07$; Mann-Whitney: $m = 50$, $n = 52$, $Z_{corr} = -0.65$, $p = 0.516$, NS). Restricting the latter comparison to data

drawn only from the appropriate <110 second window and/or those subjects possessing more accurate scores (at least 3 eligible PC/MC pairs) did not alter this outcome.

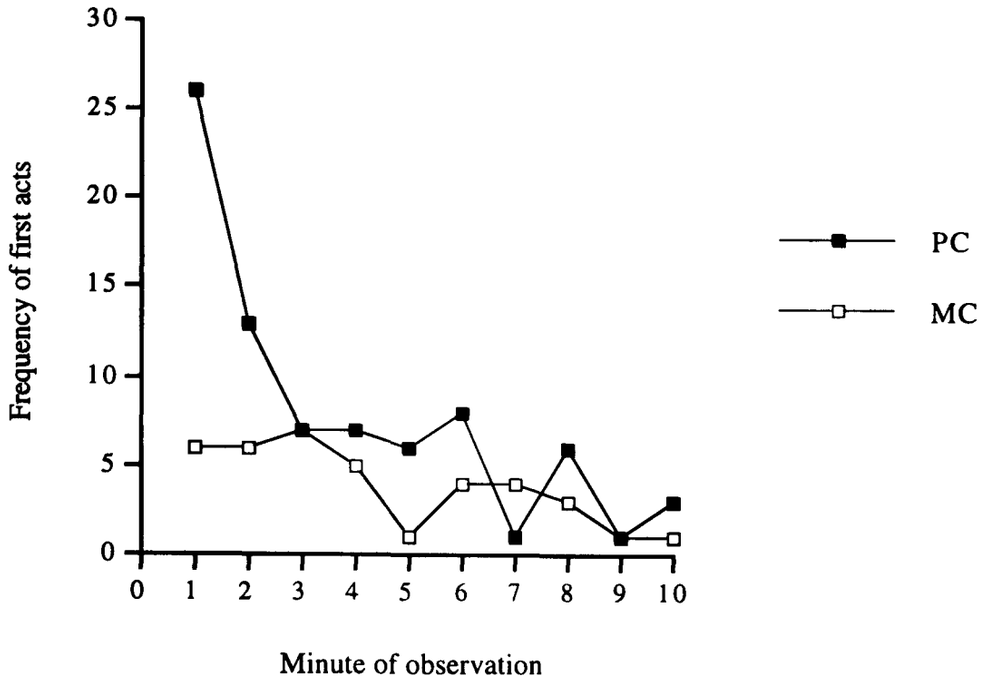



*Figure 5.2.* Distribution over time of first affiliative interactions with opponent's kin bystanders in aggregate post-conflict (PC) versus matched-control (MC) observations. For each observation, only the first interaction between the subject and an individual from this partner class has been taken into account. From 320 PC/MC pairs.

Subjects from younger age cohorts exhibited higher levels of post-conflict affiliation with relatives of their initial opponents. Although no significant correlation was found between individual AT scores and subject age when all eligible individuals were examined (Spearman: $N = 102$, $r_s = -0.10$, $p = 0.304$, NS), a significant negative correlation existed when the test was limited to only the more accurate scores of individuals possessing 3 or more PC/MC pairs (Spearman: $N = 56$, $r_s = -0.30$, $p = 0.026$). This result has been regarded as significant even though the preferred criterion of $p \leq 0.025$ for a second test was not attained, partly because a full Bonferroni correction would be excessively harsh for such a partially independent test (see chapter 2), but also because in cases where the second test has been performed on more accurate individual scores the consequent restriction of sample size (see above) itself biases against spuriously achieving significance in a subsequent test (i.e. this situation differs somewhat from those second tests where a comparison was simply repeated on data drawn from within an earlier time "window", and for which this adjustment of the alpha criterion was introduced).

Finally, an early increase in affiliation with kin of the initial opponent under post-conflict conditions could be demonstrated both when the focal subject had been the aggressor in

the preceding conflict, and when the subject had been the former victim (aggressors: 19.1% EP and 7.0% LP; Wilcoxon: $N = 57$, $Z = -2.53$, $p = 0.012$; victims: 26.3% EP and 9.0% LP; $N = 71$, $Z = -2.41$, $p = 0.016$). For individuals which possessed PC/MC pairs for both roles, there was a nonsignificant trend for the tendency to affiliate with a member of the opponent's kin to be more elevated after conflicts in which the subject had been the victim ($AT_{aggr} = 0.11 \pm 0.06$, $AT_{vict} = 0.28 \pm 0.09$; Wilcoxon: $N = 35$, $Z = -1.69$, $p = 0.091$, NS). This result remained a nonsignificant trend if the test was limited to data from the initial <110s window, and/or restricted to the few individuals which possessed two or more eligible pairs both as a former aggressor and as a former victim.

*Initiative*

To investigate whether the former combatant or the bystander tended to establish affiliative interactions, and whether the responsibility for initiation differed according to the focal animal's role in the prior conflict, first acts occurring within the <110 second window in PCs were examined. Of 38 such first acts in the PCs, the majority (68.4%) were instigated by the immature contestant. This was very similar to the pattern of initiative exhibited in the MCs, where all 38 first acts occurring at any point in the 10-minute observation could be utilised - 71.1% being initiated by the young contestant. Post-conflict initiative did not differ appreciably according to a subject's role in the preceding dispute; following unidirectional conflicts in which the subject had been the aggressor 63.6% of 11 first acts occurring within the first 110 seconds were initiated by the contestant, and following those in which the subject had been the victim 61.5% of 13 first acts were instigated by the contestant. In all 3 cases, very similar figures were obtained if the sample of first acts was increased by utilising all 78 first acts occurring at any point in the 10-minute duration of the PCs. The social partners involved in these first interactions between focal animals and relatives of the initial opponent were typically younger (69.2% of 78 first PC affinitive events being with such a partner; rising to 76.3% if only the 38 first acts which occurred within the <110 second PC window were used) than the former adversary itself had been. In the MCs, as might be expected, approximately half the 38 first affiliative events (55.3%) involved partners younger than the initial opponent and half involved peers or older interactants. The above figures concerning relative age of partners were similar whether the subject was a previous aggressor or previous victim (in uni-directional conflicts), as well as when cases were split according to whether the subject or the bystander had taken the initiative.

## *Affiliation with nonkin group members*

When considering affinitive interactions between subjects and nonkin third parties (individuals which were neither involved in the original conflict, nor members of either

the subject's or the initial opponent's extended matrilines), it transpired that a general increase in affiliation with most group members did exist under post-conflict conditions. Even with this category of partners, the proportion of "earlier" pairs was significantly greater than that of "later" pairs at the individual level (18.4% EP versus 10.9% LP, of a total of 423 pairs; Wilcoxon: $N = 107$, $Z = -2.61$, $p = 0.009$). Mean affiliative tendency with these nonkin partners was 0.08 ($N = 107$ individuals), and 64.8% of the total of 88 first bouts occurring in the PC observations involved physical contact.

Figure 5.3 presents the frequency distribution of first acts across time in PCs and MCs; the difference between the two relative cumulative frequency distributions was significant (Kolmogorov-Smirnov: $m = 88$, $n = 62$, $X^2 = 18.70$, $df = 2$, $p < 0.001$, 1-tailed), with the maximal difference being located at <140 seconds. Once again this time window was also representative of the behaviour of individuals, as the proportion of PCs in which the first affinitive interaction between a subject and a nonkin bystander occurred within <140 seconds was significantly greater than the equivalent proportion of the same subject's MC observations (PC = 0.11 ± 0.02, MC = 0.02 ± 0.01; Wilcoxon: $N = 107$, $Z = -4.07$, $p = 0.000$).

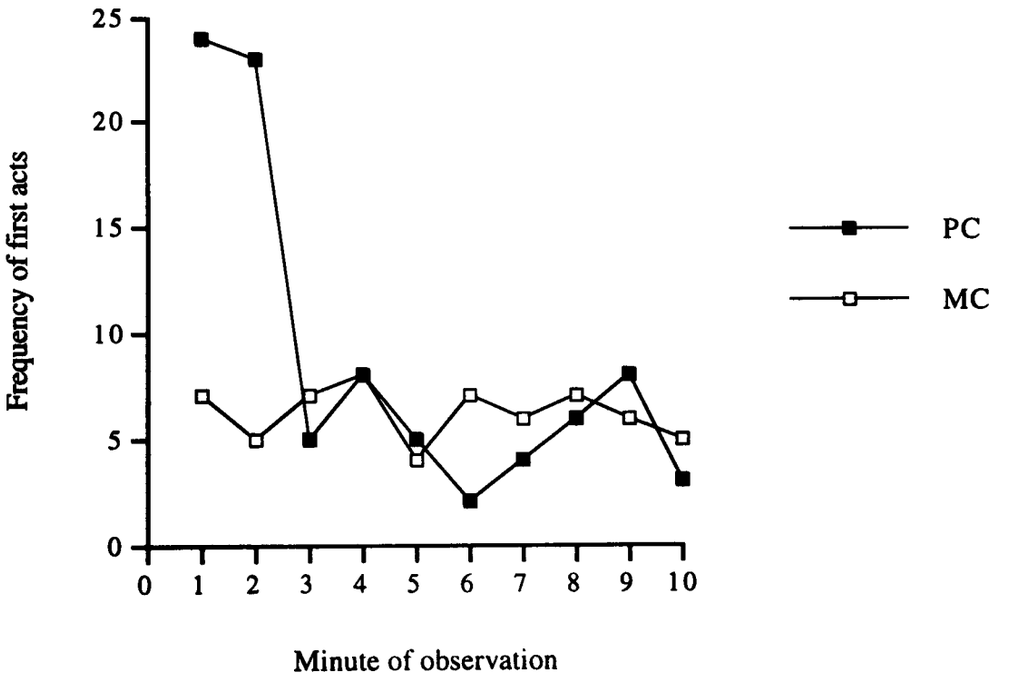



*Figure 5.3.* Distribution over time of first affiliative interactions with nonkin bystanders in aggregate post-conflict (PC) versus matched-control (MC) observations. For each observation, only the first interaction between the subject and an individual from this partner class has been taken into account. From 423 PC/MC pairs.

*Subject attributes and role in conflict*

The post-conflict increase found in affiliative interactions between nonkin was representative of both sexes. In both cases, the PC-MC method produced only a nonsignificant trend toward earlier affinitive interactions when performed using the full 10-minute observation period (males: 22.7% EP and 13.5% LP; Wilcoxon: $N = 54$, $Z = -1.83$, $p = 0.067$, NS; females: 14.4% EP and 8.3% LP; $N = 53$, $Z = -1.81$, $p = 0.070$, NS), whereas a significant effect was discerned when the test was performed within the relevant <140 second time window (males: 13.8% EP and 3.7% LP; Wilcoxon: $N = 54$, $Z = -3.12$, $p = 0.002$; females: 8.3% EP and 1.4% LP; $N = 53$, $Z = -2.67$, $p = 0.008$). Furthermore, affiliative tendency ($AT_{male} = 0.09 \pm 0.05$, $AT_{fem} = 0.07 \pm 0.04$) did not differ significantly according to sex of the focal subject (Mann-Whitney: $m = 54$, $n = 53$, $Z_{corr} = -0.64$, $p = 0.521$, NS). Restricting the comparison to the appropriate <140 second time-frame and individuals possessing at least 3 eligible PC/MC pairs did not alter this outcome.

Individual affiliative tendencies did not vary significantly with age of the focal subject. No significant correlation was exhibited between AT scores with respect to nonkin bystanders and subject age in years (Spearman: $N = 107$, $r_s = 0.03$, $p = 0.777$, NS), and checking this result by performing the test within the initial <140 second period whilst using only those individuals with 3 or more PC/MC pairs confirmed that age did not have any significant effect.

Finally, both former aggressors and former victims exhibited a post-conflict tendency to engage in affiliation with nonkin third parties. Although the number of "earlier" pairs was not significantly greater than that of "later" pairs when the test was conducted over the full 10 minutes (aggressors: 15.3% EP and 9.7% LP; Wilcoxon: $N = 64$, $Z = -1.82$, $p = 0.069$, NS; victims: 20.3% EP and 11.8% LP; $N = 85$, $Z = -1.41$, $p = 0.158$, NS), in both cases a significant result was obtained when the comparison was restricted to the relevant initial time window (aggressors: 9.5% EP and 2.0% LP in first <140 sec; Wilcoxon: $N = 66$, $Z = -2.75$, $p = 0.006$; victims: 11.9% EP and 3.6% LP; $N = 88$, $Z = -2.58$, $p = 0.010$). For individuals sampled in both roles, no significant difference in affiliative tendency was discerned following conflicts as a former aggressor versus those as a former victim ($AT_{aggr} = 0.08 \pm 0.05$, $AT_{vict} = 0.08 \pm 0.07$; Wilcoxon: $N = 50$, $Z = -0.01$, $p = 0.994$, NS). Limiting this comparison to data from the initial <140 second period and individuals possessing 2 or more eligible PC/MC pairs in each role did not alter this result.

### *Selective affiliation with specific classes of third party*

#### *Own kin bystanders*

Post-conflict affiliation occurred disproportionately between a subject and its own relatives, and was not merely a side effect of the generally increased tendency to engage in affinitive interactions. Individual affiliative tendencies with related third parties were significantly greater than those with nonkin bystanders ($AT_{own} = 0.25 \pm 0.05$, $AT_{non} = 0.09 \pm 0.03$; Wilcoxon: $N = 99$, $Z = -2.66$, $p = 0.008$).

However, although both male and female subjects had exhibited a significant PC increase in affiliation with their own kin, females had exhibited a significantly greater tendency than males. Therefore it is possible that the selectivity toward own kin partners demonstrated above is due to its presence in females alone, with no selective increase occurring in males. Performing the test separately for male and female subjects revealed significant selectivity in females ($AT_{own} = 0.26 \pm 0.05$, $AT_{non} = 0.08 \pm 0.03$; Wilcoxon: $N = 50$, $Z = -2.79$, $p = 0.005$) but not in males ($AT_{own} = 0.11 \pm 0.06$, $AT_{non} = 0.09 \pm 0.03$; Wilcoxon: $N = 49$, $Z = -0.64$, $p = 0.525$, NS); these comparisons were conducted using data from the <110s initial window, as this was the time-frame over which the PC increase with respect to own kin bystanders was most pronounced and in which a significant sex difference had been discerned. Checking the male result by limiting the comparison to the more accurate scores of individuals possessing ≥3 eligible PC/MC pairs (with both types of partner) did not alter this outcome. Finally, if the magnitude of the difference in affiliative tendency with own- versus non-kin bystanders ($AT_{own} - AT_{non}$) was directly compared between males and females over the first 110 seconds, female subjects exhibited a strong trend toward greater selectivity than males (females: $0.185 \pm 0.059$, males: $0.018 \pm 0.065$; Mann-Whitney: $m = 49$, $n = 50$, $Z_{corr} = -1.94$, $p = 0.052$). Checking this result using the more accurate scores of individuals possessing ≥3 eligible PC/MC pairs confirmed its significance (females: $0.256 \pm 0.057$, males: $0.003 \pm 0.063$; Mann-Whitney: $m = 26$, $n = 25$, $Z_{corr} = -2.66$, $p = 0.008$).

#### *Opponent's kin bystanders*

The post-conflict increase in affiliation between subjects and bystanders related to their initial opponent was also selective. Individual affiliative tendencies with the opponent's close kin were significantly greater than those with nonkin bystanders ($AT_{oppt} = 0.17 \pm 0.04$, $AT_{non} = 0.06 \pm 0.03$; Wilcoxon: $N = 101$, $Z = -2.28$, $p = 0.023$). Given that subjects of both sexes had exhibited a post-conflict increase in affinitive interactions with kin of their opponents and with nonkin bystanders, and in neither case did affiliative tendencies differ significantly between the sexes, the selectivity test was not repeated separately for male and female immatures.

## *Further investigation of PC affiliation with opponent's kin bystanders*

### *Side-effect of direct reconciliation?*

To exclude the possibility that the occurrence of affiliation between subjects and kin of their initial opponents was simply a side effect of proximity to and/or reconciliation with the opponent itself, the PC-MC comparison was restricted to those pairs in which no approach (to ≤0.6m) or affiliative act had taken place between the initial opponents before, or at the same time as, the occurrence of any affiliation (or of any approach preceding that affiliation) with the initial opponent's kin in the same observation. Even in this subset of the data there was a significant PC elevation of affiliation between subjects and relatives of their initial opponent (19.7% EP versus 7.3% LP, of 300 eligible PC/MC pairs; Wilcoxon: $N = 99$, $Z = -3.09$, $p = 0.002$).

### *Relation to identity of individuals in proximity*

Nor did the increase in affiliation between subjects and relatives of their initial opponent under post-conflict conditions appear to be due simply to the over-representation of such partners in the immediate vicinity. Focal immatures were not more likely to be involved in affiliation with close relatives of their former opponent following conflicts in which at least one member of the opponent's family had been present (as a bystander) within a 5 metre radius at the start of the PC, than those where there had been no relatives of the opponent within this level of proximity - individual affiliative tendencies did not differ significantly between the two situations ($AT_{present} = 0.19 \pm 0.06$, $AT_{absent} = 0.12 \pm 0.05$; Wilcoxon: $N = 59$, $Z = -1.01$, $p = 0.315$, NS). This comparison also remained nonsignificant when restricted to the more accurate scores of individuals possessing at least 2 eligible PC/MC pairs of each type. Furthermore, when the identity of the partner involved in the first post-conflict bout of affiliation with opponent's kin was examined, it transpired that in at least half the cases (54.4%) that particular individual had not been within a 5m radius at the start of the observation, even if other members of the opponent's family had been.

Taken together, the above results demonstrate not only that post-conflict affiliation with relatives of the previous opponent is selectively increased, but also suggest that its occurrence is unlikely to have been merely a side-effect of attraction between the former opponents themselves, nor due to the over-representation of members of the opponent's family in the immediate vicinity at the termination of the conflict.

## *Discussion*

Following conflicts, immature subjects were involved in affiliation with third parties (TPA) at significantly elevated rates. This result held for all three partner classes examined, including bystanders unrelated to either of the original protagonists. Nevertheless, these post-conflict increases were significantly biased toward partners maternally related to either the subject or to its primary opponent. Where related bystanders were concerned the latter statement held only for female contestants and not males, whilst both sexes exhibited a selective post-conflict increase in affiliation with relatives of former opponents. Younger contestants appeared more likely to be involved in TPA with the opponent's kin, but age did not exert any significant effect upon the tendency of immature subjects to initiate or receive affiliation from their own relatives. Finally, a subject's role in the preceding confrontation did not appear to have a marked effect upon the likelihood of TPA taking place, and responsibility for initiating interactions resided mainly with contestants (as opposed to bystanders), irrespective of the former's role as aggressor or victim.

### *Affiliation with related bystanders*

A selective increase in affiliation between subjects and their own close relatives was observed under post-conflict conditions. This bias toward related third parties was demonstrable despite the fact that, following polyadic disputes, interactions with former supporters (which were often close relatives of the beneficiary; see chapter 3) were not included in the analysis, and thus the extent of post-conflict affiliation between contestants and their relatives was likely to have been slightly underestimated. The majority (approximately two thirds) of these post-conflict events were instigated by contest participants, a proportion which did not differ appreciably depending upon the immature subject's role in the previous conflict, and was similar to the pattern of responsibility exhibited under baseline conditions. These results are consistent with previous reports that young primates often seek the company of their close kin after receiving aggression (e.g. Pereira 1993, Watts 1995b, Weaver & de Waal, in press), although in the present study both aggressors and victims appeared to take part in such family reunions. Similar post-conflict increases in affinitive exchanges between former contestants and their maternal relatives have been documented in a minority of controlled studies which utilised mixed-age samples (pigtail macaque aggressors: Judge 1991, Guinea baboon victims: Petit & Thierry 1994c), although in some studies evidence as to whether or not affiliation was actually biased toward these relatives was not presented (e.g. Cheney & Seyfarth 1989), and the majority of studies which examined former victims in a variety of macaque species found no evidence of this phenomenon (e.g. Judge 1991, Aureli 1992, Aureli *et al.* 1993, 1994). Information regarding the

selectivity of these contacts is vital before concluding that kin partners are prioritised; as Das *et al.* (1997) have recently demonstrated, the existence of a significant post-conflict increase in interactions with related third parties (in this case by female longtailed macaque aggressors) need not necessarily imply that affiliation is in any way biased toward these particular bystanders.

As expected, the types of third party affiliates favoured differed systematically between male and female contestants. Although interactions with both kin and nonkin bystanders were significantly elevated in subjects of both sexes following conflicts, only in females was such affiliation disproportionately directed toward their own relatives. Immature male subjects instead displayed a greater disposition toward interacting with nonkin partners than did females (see Das *et al.* 1997 for a similar trend in adult longtailed macaques), and no selective bias toward kin partners was detected in males. This pattern reflects association preferences exhibited under baseline conditions, and is in accordance with theoretical considerations regarding the relative importance of kin bonds to male and female macaques (for further details and associated references, refer to discussion section in chapter 3). In brief, in species which exhibit female natal philopatry and matrilineal inheritance of rank among females, young females become integrated into the matrilineal kin network at an early age, maintaining proximity to and strong affiliative bonds with their close relatives (Berman 1982, Ehardt & Bernstein 1987, Nakamichi 1989). In contrast young males are typically more peer oriented and less prone to associate with their adult female relatives, instead affiliating predominantly with brothers and unrelated males, and eventually emigrating once puberty is reached (see also Colvin 1983, Pereira 1988a, van Noordwijk *et al.* 1993, Nikolei & Borries 1997). If youngsters turn primarily to - or are approached by - their favoured associates for reassurance or protection in the wake of conflicts, then only in female immatures should family members be disproportionately represented among the bystanders contacted.

A high proportion of first affiliative events between subjects and their own kin involved body contact (88.2%) and it is possible, although as yet untested, that contestants may reduce the physiological costs of participation in aggression via the calming effect that peaceful contact with familiar associates can provide (cf. "reassurance": de Waal 1989a). Both aggressors, which may be aroused by their exertions, and victims, which additionally may be distressed and anxious about future events (see chapter 4), might therefore benefit. For example, under normal circumstances the somatosensory stimulation created by grooming is known to prompt the release of endogenous opiates in the recipient (Keverne *et al.* 1989) for whom it is likely to be an intrinsically rewarding activity, and is also associated with a decline in indicators of autonomic activation such as heart rate and self-scratching behaviour (Schino *et al.* 1988, Boccia *et al.* 1989, Aureli *et al.* 1999). However Das and colleagues (1998) have recently shown that post-conflict affiliation with either the relatives of one's opponent or unrelated bystanders does not

rapidly reduce post-conflict rates of scratching, at least in former aggressors. Apparently only reconciliation with the opponent itself can achieve a significant reduction in this behavioural indicator of sympathetic activation, perhaps because only an affirming interaction with the former adversary can truly allay a contestant's uncertainty about the other's future behaviour. Nevertheless, it is former victims which exhibit the highest levels of self-directed behaviour following conflicts, and which have most to fear in terms of the danger of receiving further attacks (chapter 4), and we do not yet know whether TPA might serve a calming and reassuring function in these particular cases (as originally proposed by de Waal & van Roosmalen 1979). Furthermore, the consequences of engaging in post-conflict contacts with one's own relatives have never been examined, and the possibility remains open that interactions with these especially familiar bystanders can achieve effects which those with other bystanders cannot.

For prior victims and participants in bidirectional disputes, both of which are known to be at increased risk of receiving further attacks in the aftermath of conflicts (chapter 4; see also Aureli & van Schaik 1991b, Cords 1992, Silk *et al.* 1996, Castles & Whiten 1998b), maintenance of proximity to likely supporters might additionally have an inhibitory effect upon the potentially aggressive behaviour of both former opponents and opportunistic bystanders - akin to the evidence provided by Watts (1995b) suggesting that post-conflict contact with unrelated male protectors may serve such a function for adult female mountain gorillas. Contestants might also be using this contact to actively recruit support in the event that the conflict is revived (as suggested by Das & van Hooff, in press, with regard to former aggressors). An apparent increase in rank and a more antagonistic disposition in youngsters, when in proximity to their mother or other powerful supporters, has been well documented in cercopithecines (e.g. Kawai 1965, de Waal 1977, Horrocks & Hunte 1983, Lee 1983). Furthermore, experimental manipulation of the apparent presence of an "audience" - in the form of an older relative - has been demonstrated to inhibit the aggressive actions of older group members towards juveniles and infants, in captive vervet and rhesus monkeys (Keddy Hector *et al.* 1989, Cheney & Seyfarth 1990c). Clearly, it is not only the immature contestant which may profit from such interaction; relatives may gain indirect fitness benefits if, by permitting or initiating affiliation, their actions have the effect of alleviating distress in and/or "passively" protecting their more vulnerable kin.

### *Involvement with relatives of the former opponent*

Affiliation between immature contestants and members of their former opponent's close family also occurred at elevated frequencies following conflicts (a pattern also documented by York & Rowell 1988, Cheney & Seyfarth 1989, Judge 1991, Das *et al.* 1997, Castles & Whiten 1998a), and these interactions were shown to be selective, that

is, they were more prevalent than the general increase in affiliation seen with all partners. A possible explanation for this phenomenon is that individuals actively use peaceful overtures as a means of preventing aggression spreading to include other members of the matrilines of the original adversaries (Judge 1991). Contestants may need to reduce the risk of receiving attacks from their opponents' families, whilst the latter may be motivated to take part in an effort to ensure that they themselves do not become the next target of a relative's former opponent. Given the patterns of post-conflict aggression observed in this study, and those reported in other cercopithecine taxa known for their rigid dominance hierarchies and relatively despotic social systems, it would seem likely that former victims and their kin would have the most to gain from initiating such interactions. After all, the perpetrators of aggression do not appear to be at risk of receiving retaliatory attacks overall (chapter 4; see also Das & van Hooff, in press, Castles & Whiten 1998b), and although there have been a few reports in macaques of victims preferentially targeting the relatives of former opponents when "redirecting" attacks (Judge 1982, Aureli & van Schaik 1991a, Aureli *et al.* 1992), no evidence for such a phenomenon was discerned in this study (chapter 6). In contrast, recent victims typically receive further aggression at high rates (chapter 4; de Waal & Yoshihara 1983, Aureli & van Schaik 1991b, Aureli 1992, Castles & Whiten 1998b; although it is not known to what extent relatives of the former aggressor were responsible), and individuals related to the previous victim appear to figure disproportionately among the targets of post-conflict attacks made by immature aggressors (see chapter 6). Whether or not such appeasement can actually reduce subsequent aggression between contestants and those bystanders which take part remains a moot point. Secondly, members of the victim's family may additionally gain if, by distracting or appeasing the aggressor, their actions can dissuade the latter from renewing its assault against their relative (Judge 1991, Das *et al.* 1997). Thus post-conflict affiliation with the aggressor might also serve as a low-cost form of protection for the victim, achieving the same ends as active defense yet without placing oneself in opposition to the aggressor or incurring the potential costs associated with the use of force. If this were the case, we might expect the relatives involved to be higher-ranking or in other respects more powerful than the victim itself, as such individuals should be less vulnerable to potential attacks from the former aggressor. Some indication for such a pattern has been found in pigtail macaques, where it was typically the mothers of recent victims which initiated TPA with former aggressors (Judge 1991).

An alternative possibility is that contestants use these interactions as a "substitute" for reconciliation with the opponent itself (Cheney & Seyfarth 1989), perhaps in cases where the latter appears unapproachable or is otherwise occupied. As an illustration, Aureli & van Schaik (1991a) found no evidence for a post-conflict increase in affiliation with the kin of opponents in adult longtailed macaque victims, but a significant effect was

discerned when juvenile subjects were considered separately (although unfortunately the issue of selectivity toward this particular partner class was not examined). These authors argued that immature recipients of aggression may find younger relatives of their opponent more accessible as social partners than the opponent itself. Several features of the current study are also consistent with such an interpretation. Firstly, the member of the opponent's family with which the subject first interacted affiliatively was typically younger (hence often also lower-ranking) than the opponent itself had been, and thus should have represented a less risky proposition. Secondly, the tendency to affiliate with the kin of opponents was significantly associated with age of the subject - younger contestants being more likely to be involved. It is plausible that this effect could be due to the age (and hence size) disparity between subjects and their opponents, with younger juveniles possessing a greater likelihood - on average - of facing opponents much older/larger than themselves, in which case the subject may have been less likely to initiate reconciliation because the opponent was relatively intimidating (a similar suggestion has been made by Watts 1995b regarding immature mountain gorillas, although small sample sizes precluded the performance of any statistical analysis). In addition, the more mature contestant may itself be less motivated to reconcile, because very young group members are relatively less valuable partners. Both factors may combine to produce low rates of reconciliation between opponents of very disparate age (see chapter 3), and these may be the cases where a young relative of the adversary is instead sought out by the immature contestant. Finally, there was a slight tendency for individuals to be involved in this type of third party affiliation more often when they had been recipients, rather than perpetrators, of aggression in the original dispute - a finding which, if confirmed in a larger dataset, might tend to favour this interpretation rather than an explanation in terms of preempting aggression (above; as in the latter case former aggressors should also exhibit high rates of this form of TPA, given that the victim's kin should have several reasons to initiate affiliation with such contestants). Nevertheless, it is not clear why such interactions would necessarily alter the aggressive disposition of a former attacker, nor how they might otherwise function as a "substitute" for reconciliation, although it is possible that simply by making it easier for the former opponents to remain near each other the chances of direct reconciliation occurring are enhanced.

Both male and female subjects exhibited operationally defined post-conflict affiliation with relatives of their opponents, suggesting that whatever the function of this behaviour it nevertheless applies to both sexes of contestant. This contrasts with the finding by Das *et al.* (1997), in a sample of adult and subadult longtailed macaques, that female aggressors exhibited a selective increase in affiliation with relatives of their victims, whilst male aggressors did not even display a post-conflict increase in such contacts. The difference in results between these two studies may well concern the age-distribution

of males sampled. In this study, the vast majority of male subjects (barring three young immigrants) still resided within their natal group, and thus possessed lifelong experience of the associations (e.g. kin bonds) existing between their groupmates, even if they themselves were not usually particularly active in strategies related to the matrilineal network. Furthermore, although immature males associate *less* with their own relatives than do their female peers (under both post-conflict and baseline conditions: see chapter 3 and results above), they do nevertheless spend time with and preferentially donate agonistic support to maternal kin, especially male siblings (Colvin & Tissier 1985, Kazem 1993, unpublished data), and thus may be regarded by others as the habitual associates of particular families. To the extent that bystanders were also responsible for initiating some proportion of the post-conflict affiliative events which took place between male contestants and members of their former opponents' matrilines, the results also suggest that the utility of affiliating with the opponents of one's relatives in this situation may operate regardless of the contestant's sex.

*Mere proximity or sophisticated cognition?*

However, does the presence of these patterns of post-conflict behaviour really imply that contestants (and/or their interactants) recognize the associations between third parties and act on that basis, or could simpler explanations suffice? Evidence is accumulating that nonhuman primates are adept at using information about such tertiary relations in the social sphere (Tomasello & Call 1997; also reviewed in Cheney & Seyfarth 1990a,b). For example, consistent choices in favour of the more dominant of two potential partners, demonstrated during female grooming- and conflict-interference (Seyfarth 1981, Pereira 1989, Cheney & Seyfarth 1990a, Chapais 1992), would suggest that adults can discriminate the relative rank of groupmates and apportion their behaviour accordingly. Similarly, Silk (1999) has demonstrated that male bonnet macaques preferentially solicit the help of individuals higher ranking than their current opponent (and not merely those dominant to the actor) when attempting to form coalitions. These observational studies are supported by experimental evidence showing that wild female chacma baboons appear surprised, and therefore pay more attention, when presented with manipulated sequences of playback calls in which the threat of a subordinate individual is closely followed by a scream from a more dominant female - a situation inconsistent with the existing rank relationship between those particular group members (Cheney *et al.* 1995a). More relevant in the present context is a body of work suggesting that individuals may also be aware of the affinitive bonds which exist between their groupmates. For example, in free-ranging Tibetan macaques "bridging behaviour" occurs in which an adult male carries an infant to a higher-ranking male, seemingly as a means of reducing the likelihood of an agonistic response by the male recipient (Deng 1993, Zhao 1996). Adult males typically have a preferred infant affiliate within the

group, and in triadic interactions recipient males were most often provided with that infant rather than with nearby alternatives (Ogawa 1995; see also Sinha 1998 for evidence of similar knowledge, regarding the preferred grooming partners of others, in female bonnet macaques). Again, there is some experimental evidence for such abilities, in particular work by Dasser (1988a,b) showing that after being trained to discriminate slides of related group members from those of unrelated dyads, captive longtailed macaques could correctly identify mother-offspring and sibling pairs in novel slides, despite wide variation in the age and sex of the individuals represented (see also Cheney & Seyfarth 1999 for recent evidence of knowledge of kinship in wild baboons).

With the exception of the few experimental studies cited above, the vast majority of available evidence for these abilities is derived from observational studies, in which it is often difficult to rule out alternative (less cognitive) interpretations. In particular, post-conflict work demonstrating kin biases in third party affiliation or redirected aggression (e.g. Cheney & Seyfarth 1986, 1989, Aureli *et al.* 1992) has often been cited as evidence that cercopithecines are aware of the close bonds which exist between particular group members, despite the fact that simpler explanations for the patterns of results obtained have usually not been considered. For example, enhanced rates of interaction between contestants and their opponent's kin under post-conflict conditions might be a side-effect of reconciliation between prior adversaries which, as noted by Das *et al.* (1997), might bring contestants into the vicinity of the opponent's kin group following conflicts and thus enhance the chances that they too would interact. However, in both this and the latter study this possibility could be discounted; subjects interacted with relatives of their former opponents at high rates even in cases where prior approaches and/or affiliative signals had not taken place between the opponents themselves. Nevertheless, if relatives of the protagonists tend to cluster at fights and are thus disproportionately represented in the vicinity, it is always possible that affiliation with this category of bystander could occur at elevated frequencies simply because of a general social arousal directed toward nearby and available partners (Cords 1997). Yet in this study, immature contestants were not more likely to engage in affiliation with relatives of former adversaries following conflicts in which at least one representative of the latter's family had been present within a 5 metre radius than those in which no family member was nearby; indeed, in at least half the cases of post-conflict affiliation observed, the particular individual contacted had not been in proximity when the dispute terminated, even if other matriline members had been. Therefore, the results seem consistent with the interpretation that the animals involved selected social partners on the basis of their knowledge of the bonds between others.

If this is the case, the results would seem to contradict the notion that young animals do not exhibit complex patterns of kin-oriented behaviour in the aftermath of conflicts, perhaps because they do not possess the requisite social knowledge, as suggested by

Cheney & Seyfarth (1986). Not only was a demonstrable increase in affiliation and a selective bias toward members of the prior opponent's matriline apparent under post-conflict conditions, but the youngest subjects were significantly more, not less, likely to exhibit this tendency. Similarly, in a study of longtailed macaques by Aureli & van Schaik (1991a), it was only in juvenile subjects that such a pattern could be demonstrated, and not in the entire mixed-age sample. Of course, as either the young contestant or the bystander (which might be a mature group member) could make the first overture, one cannot say with certainty that immature individuals understand the kin relations of others. However, it is worth bearing in mind that the majority of first acts were in fact instigated by the young contestant, and although this issue was not pursued with reference to the age of focal subjects, yearlings comprised almost half the study sample. At the end of the day, experiments are required to provide the controls and conditions needed to fully investigate whether or not even weanlings possess such knowledge of their social network (Kummer *et al.* 1990, de Waal 1991b). This topic which would seem to merit further investigation given that we currently know very little about the ontogeny of social knowledge and the skills which rely upon it, despite several decades of similar research undertaken on adult cercopithecines (Tomasello & Call 1997).

# 6

## *Post-conflict aggression against third parties*

### *Introduction*

In many species, an individual which finds itself in a losing position may interrupt a conflict to lash out aggressively at an innocent bystander, or do so immediately after hostilities with the original opponent have ceased. Such "redirected" aggression (Bastock *et al.* 1953; henceforth simply redirection) is often directed at a member of another species, which may not even be an ecological competitor but does tend to be a smaller and inoffensive individual, both literally and figuratively, and therefore a relatively safe target (Moynihan 1998). In socially living primates, however, redirection is most commonly directed toward a lower-ranking group member and therefore is usually intraspecific. This phenomenon has been described in many members of the genus *Macaca* (see Scucchi *et al.* 1988 for a review of relevant literature), and documented in several controlled post-conflict studies (being inferred in rhesus macaques: de Waal & Yoshihara 1983, and operationally demonstrated in longtailed and Japanese macaques: e.g. Aureli & van Schaik 1991a, Aureli 1992, Aureli *et al.* 1993). Redirection is thought to be particularly likely to occur in species such as the above, in which the fact that aggression is typically directed down the hierarchy and dominants are likely to be supported by both kin and nonkin against subordinates which attempt to contravene the established hierarchy, mean that direct retaliation against aggressors is uncommon (see e.g. Thierry 1986, de Waal & Luttrell 1989, Chaffin *et al.* 1995). This may explain why operationally defined redirection has not been demonstrated, or appears confined to only certain age-sex classes, in taxa where bidirectional conflicts are relatively more frequent (see e.g. Kappeler 1993, Watts 1995b, Castles & Whiten 1998a), although no study has so far examined whether victims are in fact less likely to redirect following conflicts in which they had retaliated against the original aggressor as opposed to those in which counteraggression had not occurred. Another possible explanation is that in such taxa the costs of redirection may also be higher, because allies of the target may be likely to support it even against higher-ranking attackers (Castles & Whiten 1998a).

A number of (not necessarily mutually exclusive) explanations have been proposed to account for this behaviour. Early descriptive accounts, together with the notion that redirection may be more common when direct retaliation against former aggressors is not an option, tend to suggest that this behaviour provides recent victims with an outlet to vent "frustration", and recent physiological and behavioural findings are consistent with the interpretation that redirection might serve as a re-regulating activity which can diminish the physiological effects of a stressor (in this case, being victimised: Sapolsky &

Ray 1989, Aureli & van Schaik 1991b). Even so, the use of aggression against conspecifics - which even when directed toward lower-ranking individuals can run the risk of injury, may provoke agonistic support in favour of the target, or create enemies within one's group - would seem to be a potentially costly way of achieving this effect. However, threats or attacks directed toward innocent third parties might produce additional short-term benefits in terms of influencing the behaviour of nearby witnesses, especially that of the former opponent. A common suggestion is that redirection can serve to distract the aggressor, focusing its attention upon a new target and thereby either terminating the initial conflict more rapidly (Gust & Gordon 1993) or reducing the likelihood of subsequent attacks against its original victim (Itani 1963, Aureli & van Schaik 1991a). Recent victims are known to be at risk of receiving further aggression from both their previous opponents and opportunistic bystanders in the minutes following escalated disputes (chapter 4; Cords 1992, Aureli & van Schaik 1991b, Castles & Whiten 1998b), but in longtailed macaques redirection behaviour has been associated with a significant reduction in the levels of aggression subsequently received (Aureli & van Schaik 1991b), perhaps because opportunistic onlookers are dissuaded by the victim's demonstration that it is nevertheless sufficiently confident and capable of immediately attacking others. This might also explain why, in the same study, redirection appeared to prompt the original aggressor to more often participate in subsequent conciliatory reunions (Aureli & van Schaik 1991a); victims capable of engaging in post-conflict aggression might constitute a greater threat to their former assailants in future. It is also possible that redirection might provide a source of leverage used to minimise the recurrence of aggression from the same opponent in the longer term, as in a number of studies there have been indications that victims specifically target relatives of their former assailant (Judge 1982, Cheney & Seyfarth 1986, Aureli & van Schaik 1991a, Aureli *et al.* 1992). Post-conflict attacks against the younger (and hence more vulnerable) kin of a former opponent inflict potential fitness costs upon the latter and consequently, if performed within view of the former aggressor, might deter future aggression from that individual (Aureli *et al.* 1992). However, as the authors acknowledge, such kin-oriented threats and attacks account for only a small fraction of all redirection events and therefore cannot provide an explanation for the general phenomenon. Finally, redirection has also been suggested to be part of a long term strategy to acquire rank as post-conflict attacks are sometimes directed against individuals which currently outrank the perpetrator, particularly where female subjects are concerned (Leonard 1979, Scucchi *et al.* 1988). Again, as such targets often characterize only a quarter of the documented post-conflict events or less this would not seem to provide a general explanation, nor one applicable to males - which in the same studies have been described as the sex more likely to respond to the receipt of aggression by redirecting.

Aggressive responses toward bystanders following conflicts have received relatively little attention in comparison to affiliative interactions between these parties, and have infrequently been examined using the methodology now regarded as appropriate in investigations of the latter (in which the latency to the first act is compared between paired post-conflict and matched-control observations). For example, renewed antagonism directed by aggressors toward their former victims has often been documented, but few studies have considered whether such contestants are also likely to attack bystanders under post-conflict conditions. Redirection of aggression by former victims has received greater scrutiny, and is known to be performed by immature as well as adult group members (being inferred in juvenile longtailed macaques: Cords 1988, and demonstrated in immature Japanese macaques and mountain gorillas: Scucchi *et al.* 1988, Watts 1995b), although juveniles appear to show less tendency to bias these attacks toward relatives of their former opponents (Cheney & Seyfarth 1986). Thus the aims of this chapter are to determine whether both former aggressors and former victims exhibit a post-conflict increase in the likelihood of threatening or attacking a bystander, whether aggressive tendency varies with the age, sex, or rank of the immature contestant, and whether or not particular types of target receive the brunt of such aggression. As in the previous chapter, the latter issue will focus upon targets related to either the subject or its former opponent and particular attention will be paid to the question of whether attacks are actually selective to these target classes.

## *Methods*

### *Definitions*

*Subject role* Following the definitions provided in chapter 3, the *aggressor* was the individual which exhibited the first aggressive act of the conflict, whilst the recipient of this initial aggressive act was termed the *victim*. All analyses in which aggressors and victims are treated separately have been restricted to those PC/MC pairs in which the direction of aggression in the original conflict had been unambiguous, i.e. counter-aggression had not occurred.

*Subject age* Refers to the focal individual's cohort age, in years (see chapter 2).

*Bystander* This term refers to all group members not involved in the original dispute, therefore excluding the original initiator and recipient of aggression and, in polyadic conflicts, any simultaneous victims, helpers or aggressive supporters of either side.

*Kinship* Individuals were classified as *close kin* if they were related through the maternal line at, or more closely than, the level of cousins (degree of relatedness $r \geq 0.0625$; note that this value assumes no inbreeding or sharing of paternal genes). For further

discussion of this definition, see chapter 3. All other individuals from the same matriline were termed *distant kin* ($0 < r < 0.0625$), whilst members of different lineages were regarded as *nonkin* ($r = 0$). In analyses, the subject's *own kin* and its *opponent's kin* refer to bystanders related at the *close kin* level to either the subject or its initial adversary, respectively. In cases where the original conflict had been between opponents from the same extended matriline a relative measure of kinship was used, such that a social partner was regarded as the subject's own kin if it was more closely related to the focal animal than to the latter's initial opponent, and as the opponent's kin if it was more closely related to the initial opponent than to the focal animal (see Judge 1991 for similar reasoning). PC/MC pairs in which the conflict had been between a mother-offspring dyad (in which, by definition, all other matriline members would be more closely related to the mother than to the offspring) or between maternal siblings (in which all social partners from the same matriline would be equally related to both opponents) therefore had to be excluded from analyses of aggression initiated against own kin and opponent's kin targets.

*Rank* Relative rank of actor and target was assessed on the basis of the overall outcome of dominance data for the specific dyad where available (see chapter 2); otherwise, status was assigned on the basis of relative position within the dominance hierarchy constructed for all immature group members (see Appendix D). Rank *position* refers to an individual's ordinal position within this hierarchy (with position 1 denoting the highest ranking immature). For certain analyses the dominance hierarchy for each group was divided into 5 equal divisions (1-5), such that individuals occupying the top 20% of positions in each group were assigned the score 1, etc., and subjects from the two study groups could be combined.

*Aggression* initiated or received refers to any overt threat or attack (e.g. facial or vocal threats, manual contact, chasing, biting), as detailed in the behavioural definitions under the heading "Agonistic interactions: aggressive" in Appendix 2. Aggressive acts between the same opponents which occurred in a sequence separated by intervals of less than 30 seconds were regarded as part of the same bout, unless the participants had engaged in a mutually exclusive act (for example by affiliating with one another) in the intervening period.

## *Data analysis*

The majority of analyses were conducted upon 441 pairs of post-conflict (PC) and matched-control (MC) observations, collected on 108 focal immatures aged between 1 and 4 years. Further details concerning data collection and the distribution of these paired observations across age, sex and conflict role categories are provided in chapter 2. Not all PC/MC pairs were suitable for use in every analysis, and specific exclusions are

outlined below. In the final analysis, concerning the effect of initiating post-conflict attacks upon the rates of aggression received from others, the PC/MC dataset was supplemented with an additional 462 10-minute post-conflict intervals derived from the 30-minute continuous observations collected on a subset of 37 focal juveniles, together with the 16 post-conflict observations for which no matched-control had been obtained. The procedure by which these conflicts were extracted from the focal observations is outlined in chapter 2, and an overview of the additional PC intervals available for each subject can be located in Appendix C.

I first examined whether immature subjects were more likely to threaten or attack previously uninvolved third parties under post-conflict (PC) as opposed to baseline (MC) conditions. Aggression initiated was analysed in a manner consistent with that used to examine post-conflict increases in affinitive interactions, again using a derivation of the PC-MC method (de Waal & Yoshihara 1983). Thus the occurrence and timing of the first bout of aggression instigated against any member of a specified target class in a PC was compared with that in the corresponding MC, each PC/MC pair being designated as either "earlier", "later" or "neutral" (see chapter 2 for further explanation of both this procedure and the following methods). Only the first aggressive act to be directed against any individual belonging to the target class of interest was utilised, per PC or MC observation. In a few PC observations (a maximum of two within any particular analysis), the first attack directed toward a bystander occurred before the start of the PC (i.e. during the initial conflict). These bouts were excluded, thus rendering the PC versus MC comparison slightly more conservative with respect to aggression against bystanders. Similarly, bouts of aggression which were directed against members of other species (e.g. lizards or birds) were not counted in analyses; although these too were more frequent under post-conflict than baseline conditions. The 13 PC/MC pairs in which one observation had been truncated before 10 minutes were utilised only when the duration of the shorter sample exceeded the time period required by the analysis (being either 10 minutes, or a shorter time window), or if the first aggressive act against a member of the partner category of interest had occurred in either the PC or MC observation before the latency at which the shorter sample terminated. A Wilcoxon signed-ranks test was then used to determine whether the proportion of "earlier" pairs (EP) was significantly greater than the proportion of "later" pairs (LP), at the individual level.

It is possible that basing the PC-MC comparison upon the entire (and arbitrary) 10-minute duration of PC/MC observations could lead to a post-conflict increase in aggression being overlooked, in cases where the baseline level of aggressive events against a particular partner class is itself high and any post-conflict increase is limited to only the first few minutes following a conflict (cf. Aureli *et al.* 1989, Veenema *et al.* 1994). The partner classes considered in this chapter may be likely to exhibit relatively high baseline levels of first interactions, due to the large number of potential targets available in each class.

Therefore I also checked for the existence and influence of any early PC increase by conducting tests using information from a shorter time-frame following the conflict. The duration of the appropriate time window (if any) was located by utilising a Kolmogorov-Smirnov two-sample test to examine whether the relative cumulative frequency distributions across time of first aggressive acts in the PCs and in the MCs differed significantly (time-rule method, Aureli *et al.* 1989). Only the first attack against any member of the specified target class was utilised, per observation. If significant, the time window was taken to be the latency (in 10 second intervals) at which, in the aggregate sample, the difference between the two relative cumulative frequency distributions was first maximal. For each category of recipient examined, the frequency distribution over time of first aggressive acts in post-conflict and in control samples has therefore been presented, and in each case the length of any applicable time window is specified. In order to check that the result obtained had not been due to the extreme behaviour of a few individuals, I also examined whether the proportion of PC observations containing at least one aggressive act against the target class of interest within this initial time window was significantly greater than the equivalent proportion of MCs, at the individual level (cf. Aureli & van Schaik 1991a).

This analysis therefore differs from several previous studies in that the time-rule was not used as a method of demonstrating whether a post-conflict increase in aggression against bystanders existed; instead, the original PC-MC comparison using individual scores was repeated upon data drawn only from the early time period identified as relevant by the time-rule, a procedure which has also recently been advocated by Das *et al.* (1997) with respect to analyses of affiliation with third parties. Whenever such a second and only partially independent PC-MC test was performed an approximate - although rather conservative - correction factor was employed, by halving the significance criterion required for the second test (i.e. $p \leq 0.025$); any cases where this more rigorous alpha level was not met have been discussed separately in the text.

I then investigated whether variables such as age, sex, rank position or role in the previous conflict influenced the degree to which post-conflict attacks against bystanders were elevated above baseline levels of interaction. Comparisons between individuals were performed using Mann-Whitney *U* tests, and based upon individual scores of corrected aggressive tendency (AT). The latter measure, analagous to the corrected conciliatory tendency index devised by Veenema *et al.* (1994), allows potential variation between individuals in baseline levels of interaction to be taken into account when calculating the post-conflict incidence of a behaviour. Aggressive tendency for an individual with respect to aggression initiated in a specific direction and toward a specific class of target is defined as (E-L)/T, where E represents the number of "earlier" pairs, L the number of "later" pairs, and T the total number of eligible PC/MC pairs possessed. However, where within-individual comparisons of aggression initiated against a

particular target class were required (e.g. of former aggressors versus victims) post-conflict data can be utilised without control, as there is no reason to believe that baseline levels of the behaviour in question would vary systematically between the two categories being compared.

In order to examine whether specific classes of bystander were targeted under post-conflict conditions, the PC-MC method was first used to ascertain whether levels of aggression directed toward [a] relatives of the initial opponent, or [b] the subject's own relatives, were elevated in the aftermath of conflicts. Matched pairs of PC and MC observations pertaining to conflicts in which the focal animal, or its initial opponent, did not possess any close relatives in the group at the time were excluded from analyses of aggression initiated against own kin or opponent's kin targets, respectively. Where a post-conflict increase in attacks against a particular class of recipient has been established, it is important to verify whether or not this result is merely due to a more general increase in such behaviour with all group members, rather than being selective to the partner category in question. Interactions with nonkin bystanders (i.e. all bystanders which did not belong to the matrilines of either the subject or its initial opponent) were used as a comparison group for this purpose (cf. chapter 5); interactions with distant kin being excluded in order to create distinct and unambiguous categories of partner (see Judge 1991, and Das *et al.* 1997, for similar logic). After establishing whether aggression against the nonkin subset of group members was enhanced under post-conflict conditions, I examined whether the increase above baseline levels with respect to opponent's kin (or own kin) targets was greater than any increase observed with nonkin targets. This was simply achieved by testing whether subjects' AT scores for the bystander class of interest were significantly greater than their AT scores with respect to nonkin bystanders. The aggressive tendency index was utilised because baseline levels of aggression directed toward different classes of partner may themselves be expected to vary depending upon the differing numbers of individuals present in each class, their likelihood of meeting, and their tendency to engage in agonistic interactions, among other factors.

To retain maximum sample size, all analyses were initially conducted using scores derived from all individuals possessing eligible PC/MC pairs, with no criterion regarding the minimum amount of data per individual. Therefore, before concluding that no significant difference existed in a particular comparison, I also checked whether the apparent lack of an effect might simply be due to limitations in the accuracy of the individual scores being used. This was achieved by restricting the comparison to subjects possessing ≥3 usable PC/MC pairs for the analysis concerned (where a within-individual comparison was involved - e.g. between conflicts as a former aggressor or former victim - this criterion had to be relaxed to ≥2 eligible pairs, because individuals were required to attain the minimum number of pairs in *each* of the categories being compared).

Next, I investigated whether post-conflict aggression might be used to preempt renewed hostilities between former opponents and/or opportunistic attacks from bystanders. These analyses were restricted to recent victims, as former aggressors did not receive aggression at elevated rates under post-conflict conditions (see chapter 4), and thus should have had less need to influence others' perception of their social position or abilities. On the basis of previous results, "redirected" aggression was operationally defined as having occurred if the first bout of aggression initiated by a former victim against a bystander took place within <130s of the preceding conflict (this being the time window within which the post-conflict increase in first attacks against bystanders had been localized). Only these "early" acts were utilised in the PCs, to guard against the possibility that first events which occurred later on in an observation (i.e. after the period when PC behaviour had returned to "normal") might influence the results. First, I examined whether redirected aggression possessed features which might increase the likelihood that such attacks would be visible and/or audible to third parties, by comparing the nature of first attacks initiated against bystanders in PCs with those initiated by the same subject in MC observations. In MC observations the first bout of aggression initiated at any point during the 10-minute period was utilised. The proportion of PC attacks against bystanders in which the former opponent was within a 5 metre radius of the subject at the point the aggression commenced was compared with the equivalent proportion of attacks from the MC observations. Proximity within 5 metres was taken to be a situation in which the former aggressor was likely to have witnessed the former victim's actions. However, it is possible that any difference obtained could have arisen simply because, as a consequence of having recently engaged in a conflict, the original adversaries were more likely to be in close proximity at the start of PCs than at the commencement of MC samples. To control for this possibility, the comparison was then limited to those pairs in which the distance between the focal individual and its opponent at the beginning of the MC had been within the same distance category (<2m, <5m, <10m, <15m or <20m) as, or in fact less than, their separation at the start of the corresponding PC. Pairs of observations in which the inter-opponent distance had been greater than 20 metres at the start of both the PC and the MC were excluded, on the grounds that relative distance could not be assessed accurately in these cases. Secondly, the proportion of PC first attacks in which the actor vocally threatened the recipient was compared with the corresponding proportion of MC first events. The use of vocal aggression was taken as increasing the likelihood that other bystanders, as well as the former aggressor, would be aware of the former victim's actions.

Finally, I examined whether post-conflict attacks by former victims against previously uninvolved bystanders were actually associated with a reduction in aggression subsequently received by the perpetrator (from former opponents and bystanders combined), using a method devised by Aureli & van Schaik (1991b). The mean rate

(bouts per minute) of aggression received in those PCs in which a redirection event had occurred ($PC^+$) was compared with that received in PCs lacking redirection ($PC^-$), at the individual level. Aggressive events occurred at only low frequency, and given that the analysis required multiple ($PC^+$ and $PC^-$) observations per individual, for this comparison the accuracy of individual scores was improved by expanding the dataset via the inclusion of post-conflict intervals drawn from the focal dataset as well as those PCs for which no MC had been obtained (see above). This was possible because the analysis was limited to a within-individual comparison of aggression initiated against one class of target; hence there would be no reason to expect that baseline levels of aggression initiated would themselves vary systematically between the categories to be compared.

Once again, redirection was defined as taking place if the subject had threatened or attacked a bystander within the first 130 seconds of the PC period. However cases in which the first aggressive act had occurred after this point in the observation were also excluded from the $PC^-$ category, in order to remove any potential influence of these later attacks. All PCs containing an affiliative interaction with the former aggressor at any point were also discarded, given that in previous studies reconciliation has itself been shown to influence the levels of post-conflict aggression received by victims (e.g. Aureli & van Schaik 1991b, Cords 1992, Castles & Whiten 1998b). Rates of aggression received were calculated only within the time-frame over which aggression received by contestants was known to be significantly elevated above baseline levels (in PCs lacking either reconciliation between opponents or aggression against bystanders: see chapter 4), this being the first 7 contiguous minutes in the overall sample of individuals, but only the initial 3 minutes for the subset of observations pertaining to former victims. The rate of aggression received in $PC^+$ periods was calculated from the point at which the first attack against a bystander took place. To provide a comparable starting point for the $PC^-$ periods, the rate of received aggression was calculated from the individual's average latency time to first redirection events onward. Nevertheless, if $PC^+$ and $PC^-$ levels of aggression received do differ significantly, it is still possible that some property of the conflict (such as its intensity or manner of termination; Aureli & van Schaik 1991b) could have caused both the redirection and the lower rates of aggression received. Therefore, I also checked whether the rates of received aggression experienced in $PC^+$ samples *before* the redirection event already differed significantly from those in $PC^-$ observations over the equivalent time-frame (i.e. before the individual's average latency to redirection).

All statistical analyses were conducted upon individual scores, and two-tailed tests were utilised throughout. The only exception concerned Kolmogorov-Smirnov tests used to estimate the time window of elevation of PC aggression, which were based upon first events occurring in the aggregate sample of observations and, given that the direction of the expected difference (i.e. a PC increase) had already been ascertained using the PC-MC method, were by definition one-tailed. Ideally, multivariate statistics would allow

simultaneous assessment of factors (such as subject age, sex, and role in previous conflict) potentially affecting aggressive tendencies toward specific classes of target. However in many cases the data did not satisfy all the assumptions of such procedures, and thus variables were examined independently using non-parametric tests. In each analysis *N* refers to the number of individuals used, whilst the total number of PC/MC pairs or PC intervals contributing towards a particular test may be presented in parentheses or in the Figure legend. Values presented refer to the mean (± SE) of individual AT scores, unless otherwise specified. The significance level was set at 5% unless a correction factor was in force, and *p*-values of between 0.05 and 0.10 are referred to as nonsignificant trends or tendencies.

## *Results*

Immature subjects initiated threats and attacks against third parties earlier following conflicts than under baseline conditions, as the proportion of "earlier" pairs was significantly greater than that of "later" pairs at the individual level (31.3% EP and 11.3% LP of 434 PC/MC pairs in total; Wilcoxon: $N = 108$, $Z = -5.28$, $p = 0.000$). Mean aggressive tendency (AT) toward bystanders was 0.18 ($N = 108$ individuals).

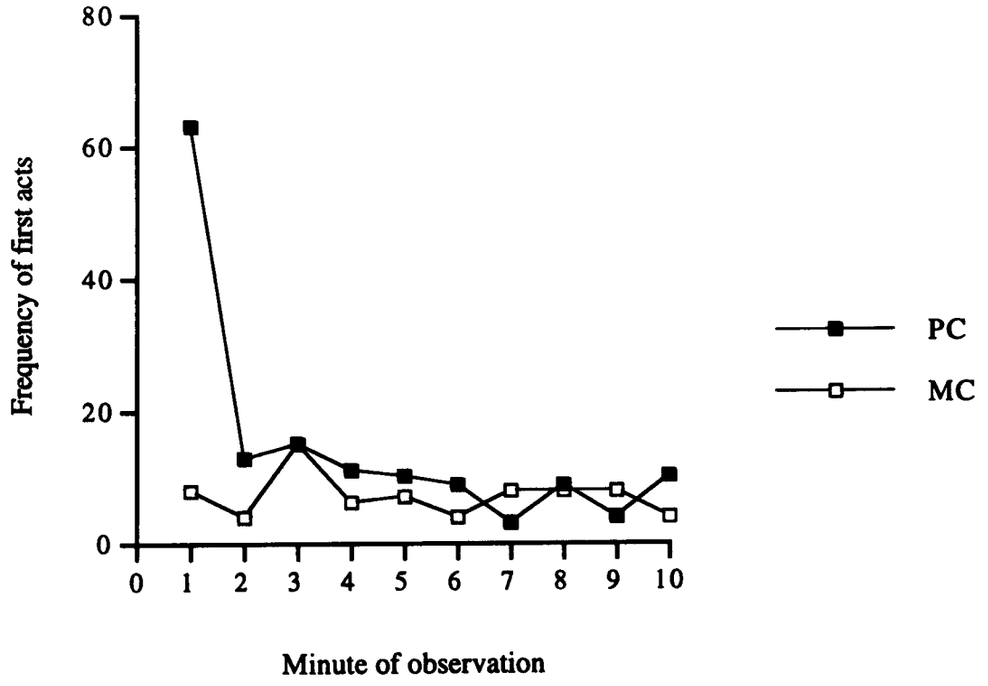



*Figure 6.1.* Distribution over time of first aggressive acts initiated against any bystander in aggregate post-conflict (PC) versus matched-control (MC) observations. For each observation, only the first attack against an individual from this target class has been taken into account. Although the Kolmogorov-Smirnov test utilised 10-sec intervals, for simplicity results have been summarised using 1-min intervals in this and subsequent figures. From 434 PC/MC pairs.

A Kolmogorov-Smirnov test revealed that the relative cumulative frequency distributions of first aggressive acts initiated in PCs and in MCs were significantly different (Fig. 6.1; $m = 147$, $n = 72$, $X^2 = 25.57$, $df = 2$, $p < 0.001$, 1-tailed), the maximal difference being located at <130 seconds after the conflict. This time window was also representative of the behaviour of individuals, as the proportion of PCs in which the first attack against a bystander occurred within <130 seconds was significantly greater than the equivalent proportion of the same subject's MC observations (PC = 0.17 ± 0.02, MC = 0.03 ± 0.01; Wilcoxon: $N = 108$, $Z = -5.30$, $p = 0.000$).

*Role in the original conflict*

To check whether the elevation of attacks against bystanders observed under post-conflict conditions was due only to the behaviour of former victims ("redirected aggression"), or exhibited by former aggressors as well, the above analysis was performed separately for each role. In both cases, significantly more aggression against previously uninvolved bystanders was displayed in PCs than in MCs (former aggressors: 31.5% EP and 11.4% LP of 149 pairs; Wilcoxon: $N = 65$, $Z = -3.23$, $p = 0.001$; former victims: 31.3% EP and 9.4% LP of 192 pairs; Wilcoxon: $N = 88$, $Z = -3.93$, $p = 0.000$). Nevertheless, the likelihood that a focal immature would initiate an attack against a third party in the PCs did in part depend upon the subject's role in the original confrontation; individuals were significantly more likely to attack bystanders if they had been the victim in the original conflict than if they had been the former aggressor (Fig. 6.2; proportion of PCs with an attack <130s: as aggressor = 0.13 ± 0.03, as victim = 0.22 ± 0.04; Wilcoxon: $N = 55$, $Z = -2.04$, $p = 0.041$). Given that post-conflict aggression initiated by former aggressors and victims may have different functions, and the fact that post-conflict levels of aggression differ according to an individual's role in the previous confrontation, subsequent analyses have also been performed whilst partitioning by role in the original conflict.

*Attributes of the immature contestant*

Both male and female subjects exhibited a significant elevation of attacks against bystanders in PC samples, following both conflicts in which they had been the former aggressor and when former victims (Table 6.1). There was no significant difference between the sexes with respect to this tendency, either when subjects had been aggressors ($AT_{male} = 0.20 \pm 0.08$, $AT_{fem} = 0.20 \pm 0.08$; Mann-Whitney: $m = 34$, $n = 31$, $Z_{corr} = -0.04$, $p = 0.972$, NS) or when victims ($AT_{male} = 0.25 \pm 0.08$, $AT_{fem} = 0.21 \pm 0.07$; Mann-Whitney: $m = 40$, $n = 48$, $Z_{corr} = -0.57$, $p = 0.567$, NS). Restricting these comparisons to data drawn from within the relevant <130 second time window and the more accurate scores of individuals possessing ≥2 eligible PC/MC pairs (in the role being considered) did not alter this outcome in either case.

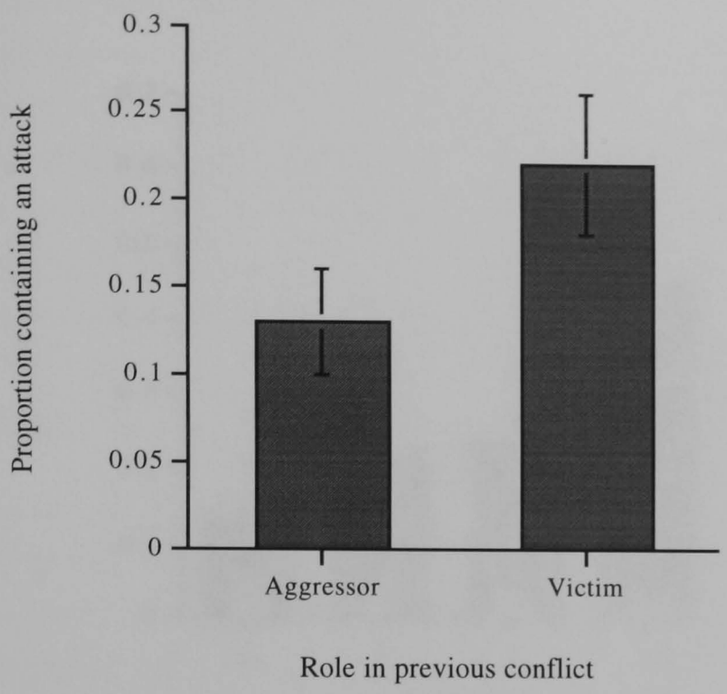



*Figure 6.2.* Mean (± SE) proportion of PC periods followed by at least one attack against a bystander within 130 seconds, by role in previous conflict. $N = 55$ individuals.

*Table 6.1.* Post-conflict increase in attacks against bystanders, according to sex and former role of subject. All PC-MC comparisons refer to Wilcoxon signed-ranks tests on individual scores.

| Subset | | *N* | *Z* | *p* |
|---|---|---|---|---|
| Male | Overall (all roles) | 54 | -3.52 | 0.000 |
| | As aggressor | 34 | -2.40 | 0.017 |
| | As victim | 40 | -2.66 | 0.008 |
| Female | Overall (all roles) | 54 | -4.10 | 0.000 |
| | As aggressor | 31 | -2.19 | 0.029 |
| | As victim | 48 | -2.91 | 0.004 |

The degree to which post-conflict aggression toward third parties was elevated above baseline levels was significantly greater in older subjects (Spearman rank correlation against age/ years: $N = 108$, $r_s = 0.24$, $p = 0.011$). Partitioning of the dataset according to the focal animal's role in the previous conflict revealed that this effect seemed to be due largely to former victims (Fig. 6.3), within which this age effect could also be demonstrated (Spearman: $N = 88$, $r_s = 0.23$, $p = 0.032$). Former aggressors did not exhibit any such age effect (Spearman: $N = 65$, $r_s = 0.17$, $p = 0.164$, NS), an outcome which remained nonsignificant when checked by restricting the test to information from within the <130 second time window and subjects possessing ≥2 eligible PC/MC pairs.

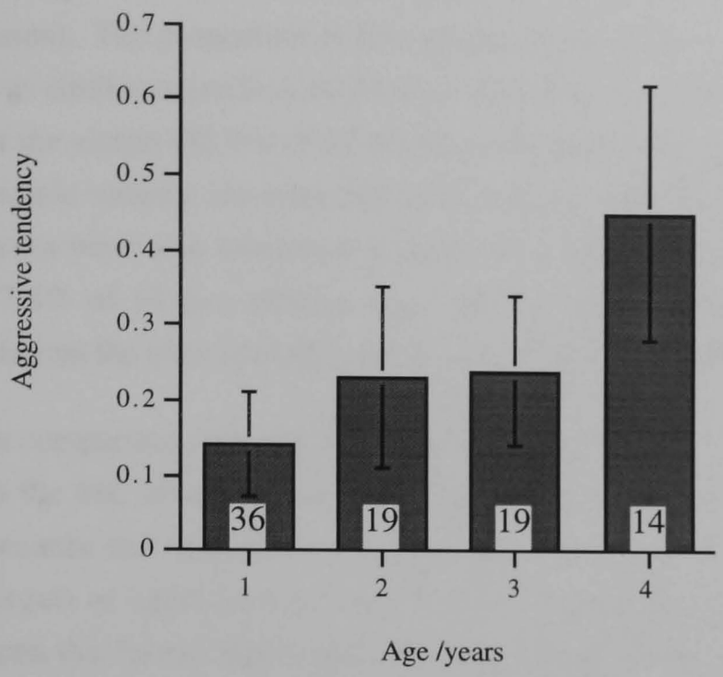



*Figure 6.3.* Mean (± SE) individual aggressive tendency for attacks directed against bystanders by former victims, according to age cohort of subject. Figures refer to the number of individuals contributing data in each cohort.

However, rank position did not appreciably influence the tendency to threaten or attack bystanders in the aftermath of conflicts, over and above its influence upon baseline levels of aggression initiated. In the overall sample, subjects from higher ranking divisions of a group did not exhibit greater aggression tendencies than lower ranking immatures (Spearman rank correlation between rank category and individual AT scores: $N = 104$, $r_s = -0.06$, $p = 0.544$, NS). Moreover, the comparison remained nonsignificant when the data pertaining to former aggressors and former victims were examined separately (aggressors: $N = 63$, $r_s = 0.03$, $p = 0.815$, NS; victims: $N = 84$, $r_s = -0.17$, $p = 0.115$, NS). In all 3 cases, checks restricted to information drawn from within the initial <130s window and limited to subjects possessing more accurate scores did not alter the outcome. Nor was there any significant effect if actual rank position (as opposed to the 5 rank divisions) was used in the analysis, and the test performed separately within each group's hierarchy.

### *The targets of post-conflict aggression*

#### *Rank relative to the subject*

As might be expected, the recipients of post-conflict aggression were typically lower-ranking than the perpetrators. Considering only those first attacks which occurred within

the initial <130s of PC observations, in 85.9% of 78 first bouts the target was lower-ranking than the immature subject (2 first attacks which involved extragroup targets having been excluded, on the grounds that relative rank could not be assigned in these cases). The proportion of first attacks in which the recipient was subordinate to the actor was similar regardless of whether the subject had been the aggressor (86.4% of 22 bouts) or the victim (83.8% of 37 bouts) in the preceding conflict. As it has been suggested that female victims are more likely to redirect aggression versus higher-ranking targets, the sexes were also examined separately in the latter subset of the data. In female victims, 77.8% of 18 first attacks were against lower-ranking group members, whilst in male victims the corresponding figure was 89.5% of 19 first bouts.

In comparison, the overall figure for the 61 first bouts of aggression initiated at any point in the MC observations was 82.0% (with an additional 11 first attacks being excluded because the aggression had been directed at a member of another group). The initial targets of aggression in those MCs corresponding to conflicts in which the subject had been the former aggressor were subordinate to the subject in 95.5% of 22 such attacks, whilst those of former victims were more subordinate in 71.4% of 21 first attacks. Thus former victims may be more likely to select a lower-ranking target when redirecting aggression than they would be when aggressing under baseline conditions. Former victims which were female also seemed more likely to select a lower-ranking target under post-conflict than baseline conditions, as only 63.6% of 11 first attacks in MCs were against a target outranked by the subject (the corresponding figure for male victims being 80.0% of 10 first attacks in the MCs), although the low frequency of MC attacks may compromise the reliability of these figures.

*Attacks against the opponent's kin, and subject's own kin*

There was a significant early increase in attacks against close relatives of the initial opponent under post-conflict conditions, in the overall sample (Table 6.2). The relative cumulative frequency distributions across time of first attacks against this subset of targets in PCs and in MCs differed significantly (Fig. 6.4a; Kolmogorov-Smirnov: $m$ = 37, $n$ = 8, $X^2$ = 11.42, $df$ = 2, $p < 0.01$, 1-tailed), with the maximal difference between the two distributions being located at <150 seconds. A comparison of the proportion of each subject's PC versus MC observations which contained a threat or attack against a close relative of their initial opponent within the first 150 seconds confirmed that this result had not merely been due to the extreme behaviour of a few individuals (PC = 0.085 ± 0.017; MC = 0.003 ± 0.003; Wilcoxon: $N$ = 102, $Z$ = -4.12, $p$ = 0.000).

*Table 6.2.* Post-conflict increases in aggression initiated against specific classes of bystander. All comparisons refer to Wilcoxon signed-ranks tests using individual scores.

| Bystander class | Time-frame used/ s | % EP | % LP | Total pairs | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|---|
| Opponent's kin | 600 | 11.2 | 1.9 | 321 | 102 | -3.23 | 0.001 |
| Own kin | 600 | 11.7 | 5.4 | 368 | 102 | -1.95 | 0.051, NS |
| | 130 | 6.3 | 0.0 | 378 | 102 | -3.17 | 0.002 |
| Nonkin | 600 | 11.1 | 6.0 | 431 | 108 | -3.28 | 0.001 |

Surprisingly, focal animals also directed significantly more aggression at their own close kin after being involved in conflicts, when compared with baseline conditions (Table 6.2). In this case a strong but nonsignificant trend toward earlier aggression in PCs was discerned when the comparison was performed over the entire 10-minute observation period, but when restricted to the initial time window of <130 seconds appropriate for aggression against kin bystanders (see below), the PC-MC comparison proved highly significant. A Kolmogorov-Smirnov test revealed that the relative cumulative frequency distributions of first attacks against related bystanders differed significantly ($m = 43$, $n = 21$, $X^2 = 14.71$, $df = 2$, $p < 0.001$, 1-tailed), with the difference first being maximal at <130 seconds after the conflict (Fig. 6.4b). A comparison of the proportion of each individual's PC versus MC observations which contained at least one bout of aggression against a close relative within the first 130 seconds confirmed that this result had not merely been due to the extreme behaviour of a few subjects (PC = 0.047 ± 0.012; MC = 0.003 ± 0.003; Wilcoxon: $N = 102$, $Z = -3.38$, $p = 0.001$), although the frequency of such aggression was low even in post-conflict observations.

Furthermore, focal animals were also significantly more likely to initiate aggression against unrelated bystanders following conflicts than they were under baseline conditions (Table 6.2), suggesting that the results presented above might merely be part of a generalized increase in aggression rather than being specific to the partner classes considered. However, there was no significant difference between the relative cumulative frequency distributions of first acts in PCs versus MCs (Fig. 6.4c; Kolmogorov-Smirnov: $m = 52$, $n = 31$, $X^2 = 2.31$, $df = 2$, $p < 0.10$, NS). Thus although there is a significant elevation of attacks against nonkin third parties under post-conflict conditions, demonstrated using the PC-MC method, this increase cannot be localised to a specific time window of less than 10 minutes following conflicts.

*Selective aggression*

Given that the patterning and function of post-conflict aggression may differ according to an individual's role in the immediately preceding confrontation, analyses examining whether these attacks were disproportionately directed toward specific categories of target were performed separately upon former aggressors and former victims. Theoretically, these tests could be performed either over the full 10-minute observation period, or within any initial time window relevant to the partner category of interest, the latter being the period over which significant selectivity is most likely to be demonstrated (Das *et al.* 1997). Therefore in order to minimise the number of potential tests to be performed, and given that a significant post-conflict increase in attacks had strictly only occurred within the initial <130s where the own kin target category was concerned, tests were simply performed within the time window relevant to the partner category of interest. In such cases it is possible that any selectivity demonstrated does extend over the entire 10-minute observation period, but one can only conclude that a selective increase exists for the duration of the time window actually tested.

The post-conflict elevation of attacks against relatives of the initial opponent (oppt) was significantly greater than the corresponding increase with respect to nonkin bystanders (non), in former aggressors (initial <150s: $AT_{oppt} = 0.099 \pm 0.028$, $AT_{non} = 0.012 \pm 0.012$; Wilcoxon: $N = 58$, $Z = -3.18$, $p = 0.002$). However former victims did not display any such selectivity (initial <150s: $AT_{oppt} = 0.029 \pm 0.017$, $AT_{non} = 0.073 \pm 0.027$; Wilcoxon: $N = 73$, $Z = -1.51$, $p = 0.132$, NS); indeed, the data were suggestive of quite the opposite tendency. The latter result remained nonsignificant when checked by restricting the comparison to the more accurate scores of individuals possessing ≥2 PC/MC pairs of each type.

A selective bias toward own kin targets (own) could not be demonstrated. Former aggressors did not exhibit any tendency to bias attacks toward their own kin (initial <130s: $AT_{own} = 0.026 \pm 0.018$, $AT_{non} = 0.014 \pm 0.012$; Wilcoxon: $N = 59$, $Z = -0.31$, $p = 0.753$, NS), an outcome which was not altered if the comparison was restricted to individuals possessing more accurate scores. Nevertheless, there was some indication that former victims might differ in this respect. In the latter subset of cases, aggression against an individual's own relatives was not selectively increased when all eligible individuals were examined (initial <130 seconds: $AT_{own} = 0.104 \pm 0.028$, $AT_{non} = 0.045 \pm 0.020$; Wilcoxon: $N = 82$, $Z = -1.58$, $p = 0.114$, NS), but a nonsignificant trend in this direction became apparent when the test was performed on the more accurate scores of subjects possessing at least 2 PC/MC pairs of each type (initial <130 seconds: $AT_{own} = 0.124 \pm 0.035$, $AT_{non} = 0.037 \pm 0.020$; Wilcoxon: $N = 45$, $Z = -1.81$, $p = 0.070$, NS). However, it should be borne in mind that some adjustment of the significance criterion is required for second only partially independent tests, and therefore

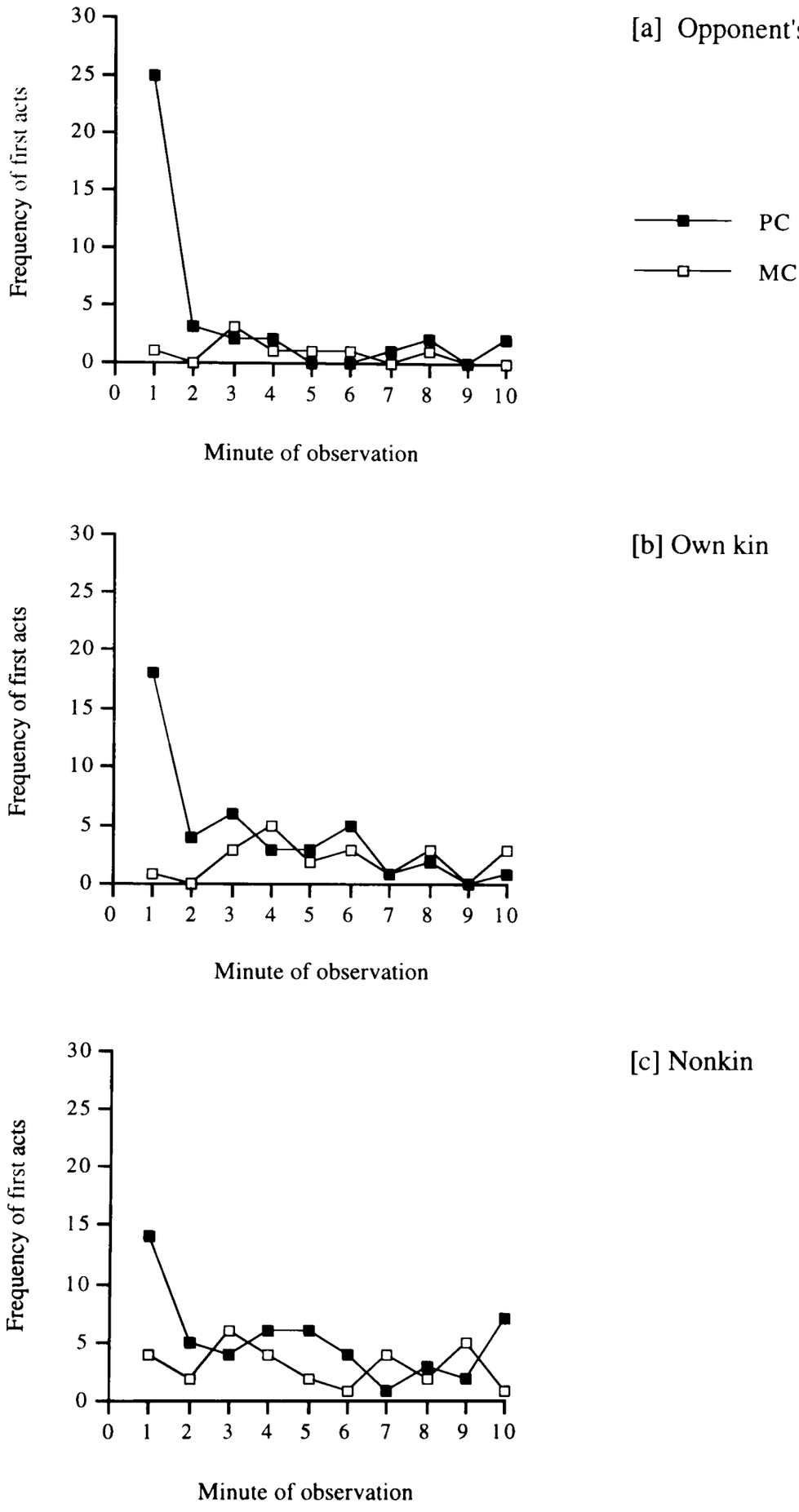



*Figure 6.4.* Distribution over time of first aggressive acts initiated against bystanders [a] related to the former opponent, [b] related to the subject, or [c] unrelated to either opponent, in aggregate post-conflict (PC) versus matched-control (MC) observations. For each observation, only the first attack against an individual from the specified target class has been taken into account. From 321, 368 and 431 PC/MC pairs, respectively.

this apparent tendency should be interpreted with caution (although, in cases such as this, the halving of sample size in the second test itself biases against the likelihood of spuriously achieving significant or near-significant results).

*Male and female former aggressors*

Finally, given that the degree of kin bias in social interactions may differ between male and female macaques, the selectivity analyses were also performed separately for subjects of each sex. This analysis was limited to former aggressors and attacks against the opponent's kin, because only in this subset of the data had a selective bias been demonstrated. In both sexes, the post-conflict increases proved to be selective (initial <150 sec: males: $AT_{oppt} = 0.059 \pm 0.025$, $AT_{non} = 0.007 \pm 0.007$; Wilcoxon: $N = 31$, $Z = -2.20$, $p = 0.028$; females: $AT_{oppt} = 0.144 \pm 0.053$, $AT_{non} = 0.019 \pm 0.026$; Wilcoxon: $N = 27$, $Z = -2.37$, $p = 0.018$). Furthermore the degree of selectivity, measured as ($AT_{oppt}$ - $AT_{nonkin}$), did not differ significantly between the sexes (initial <150 sec: $0.053 \pm 0.024$ versus $0.126 \pm 0.048$, Mann-Whitney: $m = 31$, $n = 27$, $Zcorr = -0.82$, $p = 0.411$, NS). This result was not altered by restricting the comparison between the sexes to individuals possessing ≥3 eligible pairs.

***Potential for redirected aggression to act as a signal to third parties***

*Presence of the former aggressor*

The mean proportion of "redirected" attacks (defined as the first aggressive act against a bystander, if initiated by a former victim within the first <130 seconds in a PC observation), in which the actor's former opponent was within a 5 metre radius when the aggression took place, was significantly greater than the corresponding proportion of first attacks initiated in MC observations (PC proportion = $0.70 \pm 0.107$, MC = $0.11 \pm 0.043$; Wilcoxon: $N = 15$, $Z = -3.11$, $p = 0.002$). To check whether this result was simply due to the former opponents tending to be closer together at the start of PC than at the start of MC observations, this analysis was also performed by restricting the test to only those observations in which the MC inter-opponent distance at the beginning of the observation was either within the same 5 metre distance category as, or a closer category than, the PC inter-opponent distance. The result still held (PC = $0.73 \pm 0.124$, MC = $0.18 \pm 0.068$; Wilcoxon: $N = 11$, $Z = -2.70$, $p = 0.007$).

*Aggressive acts used*

The mean proportion of operationally defined redirected attacks in which the former victim vocally threatened its target was significantly greater than the corresponding

proportion of first attacks initiated in MC observations (PC proportion = 0.62 ± 0.118, MC = 0.29 ± 0.085; Wilcoxon: $N = 17$, $Z = -2.20$, $p = 0.028$). Therefore redirected aggression potentially creates a situation in which third parties not in the immediate vicinity may be more likely to perceive the former victim as an "aggressor" and less likely to perceive that individual as a "victim". However redirected aggression does not appear to create "new" victims, in that the mean proportion of redirected attacks which caused the target to scream was not greater than the proportion of first attacks in MCs in which the recipient responded with screams; indeed there was a strong trend in the opposite direction (PC proportion = 0.18 ± 0.095, MC = 0.41 ± 0.093; Wilcoxon: $N = 17$, $Z = -1.89$, $p = 0.059$, NS). This latter trend might have been due to systematic differences between PC and MC first attacks in the average intensity of aggression used by the focal subject, for example if the preponderance of vocal threats in post-conflict aggression meant that these bouts were of slightly lower intensity than baseline first bouts (which might additionally involve chasing or contact aggression).

*Aggression received after redirection events*

Redirection of aggression by former victims was associated with a significant reduction in the amount of aggression subsequently received from previous opponents and/or bystanders. There were 44 post-conflict observations in which there had been a redirection event against a bystander within the first <130s but no reconciliation between the former opponents ($PC^+$), and there were a further 230 post-conflict observations in which there had been neither reconciliation between opponents nor aggression initiated against bystanders at any point in the 10-minute observation ($PC^-$) available on the same subjects. When rates of aggression received were calculated across the first 7 minutes of PC observations, the mean rate received after redirection events ($PC^+$) was not significantly lower than that from the point of the individual mean latency to redirection onward ($PC^-$) in observations lacking redirection ($PC^+$ = 0.03 ± 0.012 bouts/min, $PC^-$ = 0.05 ± 0.013; Wilcoxon: $N = 26$, $Z = -0.97$, $p = 0.334$, NS). However, when the shorter timespan of 3 minutes was utilised - the time window specifically relevant to aggression received by former victims - the comparison proved significant (Fig. 6.5; $PC^+$ = 0.03 ± 0.015, $PC^-$ = 0.10 ± 0.026 bouts/min; $N = 31$, $Z = -2.28$, $p = 0.023$), even after allowing for the adjustment of the significance criterion required due to performance of a second test within a shorter window.

Nevertheless, it is still possible that conflicts which lead to redirection differ systematically in some way from those which are not followed by such events and that this leads to both the redirection and the lower rates of aggression received, rather than the redirection causing the reduction in attacks received. In fact, the intensity of the

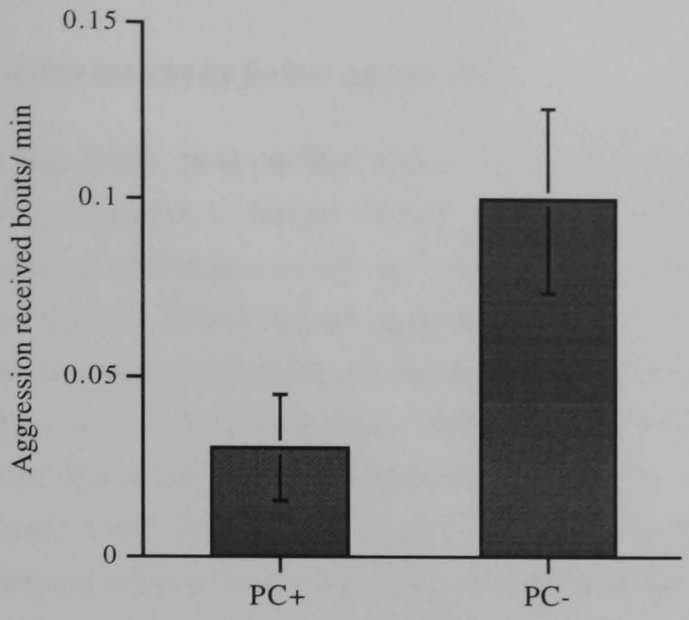



*Figure 6.5.* Mean (± SE) rate of aggression received per minute by former victims following redirection events in post-conflict observations ($PC^+$), and after the mean individual latency to redirection in observations without redirection ($PC^-$). Rates have been calculated within the first 3 minutes of PC observations; $N = 31$ individuals.

original conflict did appear to influence the likelihood of redirection taking place; individual aggressive tendencies were significantly greater following low intensity conflicts as opposed to more severe aggressive incidents ($AT_{low} = 0.36 \pm 0.08$, $AT_{high} = 0.09 \pm 0.08$; Wilcoxon: $N = 36$, $Z = -2.41$, $p = 0.016$). However, the intensity of the original conflict was not in itself associated with receiving lower levels of post-conflict aggression; in PC observations which lacked both reconciliation and aggression against bystanders, former victims did not receive lower levels of aggression following mild conflicts as opposed to severe conflicts (bouts/min calculated over initial 3 minutes: $PC_{low} = 0.05 \pm 0.026$, $PC_{high} = 0.05 \pm 0.023$; Wilcoxon: $N = 18$, $Z = -0.08$, $p = 0.933$, NS). Furthermore, returning to the main analysis, the rates of aggression received in the period *before* redirection events ($PC^+_{bef} = 0.15 \pm 0.061$ bouts/min) did not differ significantly from those over the same period in PCs lacking redirection ($PC^-_{bef} = 0.18 \pm 0.121$; Wilcoxon: $N = 31$, $Z = -0.86$, $p = 0.388$, NS), although few events occurred within such a short timespan. Therefore there is no reason to assume that the situation before redirection is different from that after conflicts which were not followed by redirection; rather, the reduction in aggression received by former victims appears to be associated with the act of redirecting itself.

## *Discussion*

*Further attacks by former aggressors*

In this study, post-conflict attacks against previously uninvolved third parties were not the prerogative of former victims, as both aggressors and bidirectional participants also initiated aggression earlier and more frequently following conflicts than under baseline conditions. Where former aggressors were concerned, the age, sex and absolute rank of the immature perpetrator did not have any significant effect upon the likelihood that such aggression would take place. Although renewed attacks by former aggressors against prior *opponents* have often been demonstrated to occur (e.g. Aureli & van Schaik 1991a, Cords 1992, Das & van Hooff, in press; see also chapter 4), increased aggression directed toward *bystanders* does not appear to have been reported in previous controlled studies of the post-conflict behaviour of former aggressors. However, not all authors which examined the initiation of post-conflict aggression separated subjects according to their role in the previous dispute in analyses (e.g. Cheney & Seyfarth 1986, 1989) thus allowing the possibility that former aggressors could have contributed to the results obtained, and few studies which did focus upon the initiators of conflicts have looked specifically for this behaviour pattern. A study by Das & van Hooff (in press) provides one exception, in which no post-conflict increase in aggression against bystanders was apparent in a mixed-age sample of longtailed macaque (*Macaca fascicularis*) aggressors.

Whilst renewed aggression against former victims may potentially be explained in terms of the aggressor underscoring its superiority over the opponent (for example because the adversary had not submitted, or had not submitted sufficiently quickly), or simply as a continuation of what is in the animal's view the same conflict, an increase in unprovoked attacks against bystanders in this situation is less readily explained. One possibility is that once an animal is already physiologically prepared to instigate aggression, it is cost effective to reinforce rank relationships against multiple individuals whilst in that state of arousal. This might explain the phenomenon of single-handed attacks versus multiple recipients - in rhesus macaques, powerful individuals such as adult males may take on entire families of females and offspring simultaneously (pers. obs.) - as well as the sequential post-conflict assaults described here. Furthermore, an individual which has recently won a bout of aggression may also be more likely to succeed in its next confrontation, thus making it particularly worthwhile to instigate further attacks at this point. In this regard it should be noted that the post-conflict analyses concerning former "aggressors" were by definition based upon starting conflicts in which aggression had been unidirectional, and all resulted in submission by the recipient; therefore in the subset of data in which the post-conflict increase was demonstrated the subject had always been the "victor" in the initial dispute.

Experimental evidence from a wide variety of taxa (predominantly rodents, fish and birds) points to the existence of such "winner effects", defined as a tendency for an individual winning one contest to subsequently win against a randomly selected and *otherwise equally matched* second individual (reviewed in Chase *et al.* 1994; see also Jackson 1991). Although the precise experimental paradigm required to demonstrate this phenomenon does not appear to have been utilised in work on nonhuman primates, patterns of agonistic interaction seen in experiments on rhesus macaques in which triads of unfamiliar individuals were placed together and their subsequent behaviour monitored were characteristic of the operation of a winner effect (Mendoza & Barchas 1983, Mendoza 1993). Specifically, double-initiate sequences - in which one individual (A) having dominated a second (B), then proceeded to also dominate the third (C) - were more frequent than expected by chance, as were double-receive patterns (if A deferred to B, then A also deferred to C: characteristic of a "loser effect"; see below) while other logically possible and intuitively probable sequences of events generally did not occur. Given that the members of each triad had been carefully matched as far as possible with respect to age, sex, size, reproductive state and general activity level, it is unlikely that double wins (or double losses) by one individual were due to intrinsic differences between the animals in attributes related to fighting ability. Rather, it may have been the differential experience of being the victor or loser in the initial encounter which influenced the patterning of events and outcome of subsequent encounters with the remaining triad member.

The physiological mechanisms which may underlie this integration of past experience are still being explored. It is possible that for a short period following a successful contest winners experience transient changes in neurotransmitter activity - for example Raleigh *et al.* (1984) have experimentally demonstrated that serotonin activity alters following changes in dominance status and aggressive behaviour; serotonin levels appear to regulate the threshold to escalate in the face of potential conflict and the intensity of aggression expressed (e.g. Mehlman *et al.* 1994, Higley *et al.* 1996). In particular, there are likely to be post-conflict alterations in circulating levels of hormones - a prime candidate being testosterone (e.g. Bernstein *et al.* 1983a). Such CNS changes may make individuals not only more likely to initiate contests, but also temporarily improve their competitive abilities. For example, a pre-contest rise (anticipating a challenge) in testosterone and/or its metabolites, and a further post-conflict rise in the eventual winner, have been documented in a number of vertebrate taxa (see Mazur & Booth 1998 and associated commentary). Increases in plasma androgen levels often mediate a swift rise in aggressive motivation, can rapidly elevate rates of cellular metabolism in muscle tissue (Tsai & Sapolsky 1996) and are known to be associated with enhancement of attention and other cognitive abilities (e.g. Hampson & Kimura 1992). These latter effects may provide a former winner with a temporary advantage over less physiologically prepared

adversaries. Finally, the winning (or conversely, losing) experience may affect how individuals amend assessments of their own fighting ability relative to the population distribution of abilities, consequently influencing their expectation of costs in future fights and therefore how likely a subject is to escalate to, or to persist during, overt aggression (Hsu & Wolf 1999). In nonhuman primates, the actual amount of aggression expressed and its outcome may have less influence upon a contestant's hormone levels and subsequent actions than does the individual's cognitive interpretation of the encounter and its perception of its current social situation (Bernstein *et al.* 1983a, Sapolsky 1998).

In addition, it is possible that third parties which witness a confrontation become less likely to challenge and/or more likely to defer to the known winner of an observed dispute, which would further reduce the costs to former victors of attacking nearby targets. Experimental evidence that birds and fish (Hogue *et al.* 1996, Oliveira *et al.* 1998) may respond in this manner after observing aggression between conspecifics in which they were not themselves involved is discussed below. Such a phenomenon cannot be ruled out in the experiments on rhesus macaque triads described previously, and might contribute toward or be responsible for the double-win patterns of interaction suggestive of the operation of a winner effect (whereas in the standard experimental procedure used to demonstrate winner effects this possibility can be excluded).

The above considerations suggest that it may be adaptive to attack others in the wake of a victory, because these attacks may be particularly likely to succeed. However, there may be additional benefits to be derived if such aggression is preferentially directed against the relatives of one's previous target. In this study a selective bias, toward kin of the former victim, was demonstrated in the post-conflict aggression instigated by victors. This result does not necessarily imply that subjects specifically selected those group members as targets; relatives of contestants often approach the scene of escalated disputes, and thus a simple rule whereby an aggressor merely targeted the nearest bystander unrelated to itself might be sufficient to ensure that kin of the victim were disproportionately targeted (for further discussion of this issue, and evidence in favour of the interpretation that choice of these interactants is cognitively mediated at least where post-conflict affiliation is concerned, see chapter 5). The utility of such attacks may be the same, irrespective of the proximate mechanism used. Firstly, a sequential assault on a clique, easily achieved if several members are particularly likely to be in the vicinity at once, enables an individual to reinforce its rank position over an entire family. The aftermath of an attack against one family member is also a situation which may provide the aggressor with useful additional information about the likely risks of any action against the remaining individuals. Close kin are the group members most likely to come to the aid of an individual involved in aggression, particularly where the more costly forms of support such as defence against assaults by more dominant individuals are concerned (Kurland 1977, Massey 1977, Bernstein & Ehardt 1985a, Kaplan *et al.* 1987). Thus if an individual was nearby yet

failed to support its relative in the preceding conflict (for whatever reason), it may be a sign that this bystander will be unlikely to put up much resistance against this particular aggressor if threatened, especially after having already witnessed its relative being beaten. In contrast, other bystanders are more of an unknown entity; there is no prior indication that a powerful supporter would not intervene in their favour if the former aggressor were to attack them, thus making them more risky targets.

Alternatively, post-conflict aggression directed against kin of a former opponent could be a tactic to preempt retaliatory attacks from those third parties. Although the aggressors considered here typically outranked their victims, the fact that the former were immature individuals means that they might nevertheless still be subordinate to older relatives of their targets, and therefore might be vulnerable to retaliation. However this explanation seems unlikely, given that former aggressors did not receive aggression at significantly elevated rates in the aftermath of conflicts (chapter 4; see also Das & van Hooff, in press, Castles & Whiten 1998b), although the frequency of attacks received from the victim's kin was not specifically examined. This result would imply that - in contrast to former victims and bidirectional participants - aggressors are unlikely to be particularly at risk in the post-conflict situation, and therefore preemptive strikes against bystanders would be unnecessary. Of course, as the above studies necessarily examined the rates of aggression received during post-conflict periods in which the subject had not itself instigated any further attacks, we cannot rule out the possibility that former aggressors *do* initiate attacks for this reason, but only on those occasions when they perceive that there is "significant" risk from bystanders. Again this would seem relatively implausible as an explanation, as it would entail assuming not only that the young subjects were virtually 100% perfect in assessing which situations required preemptive strikes, but also that any attacks initiated were always successful in preventing the receipt of aggression. However, the above suggestions regarding the immediate consequences and function of the post-conflict attacks instigated by former aggressors would be amenable to tests, and perhaps could be explored in future studies.

*Redirection of aggression by former victims*

Subjects were most likely to instigate post-conflict aggression against bystanders following those incidents in which the former had been the victim. Such redirection of received attacks toward "scapegoats" appears to be a pervasive phenomenon in many taxa, although reports often concern interspecific events with the butt of aggression being a member of a smaller species and hence a relatively safe target (Moynihan 1998). Likewise, when redirection takes place among conspecifics it is most often directed toward lower-ranking groupmates (e.g. Lindburg 1971, Scucchi *et al.* 1988, Sapolsky 1998), which should be comparatively unlikely to retaliate. Both aspects are well

conveyed by the description of tensions between wild hyaenas at a kill as a chain of aggression in which "hyena A chases B, B chases C, C chases D, and D chases vultures" (Zabel *et al.* 1992, p. 129). In this study too, the majority of first aggressive acts performed by former victims were against targets currently subordinate to the actor, as might be expected given that in rhesus macaques aggression tends to be directed down the hierarchy under most circumstances (e.g. Bernstein *et al.* 1983b, Thierry 1986, de Waal & Luttrell 1989), and especially given that the perpetrator is itself in a relatively vulnerable position due to having recently been threatened or attacked (see chapter 4). Therefore it seems unlikely that subjects would be utilising these acts as a means of acquiring rank, as has been postulated for female macaques (Leonard 1979, Scucchi *et al.* 1988), especially as redirection events were less frequently directed against group members which outranked the actor than were threats or attacks instigated under baseline conditions (although no formal test of this issue was conducted). Nor did male and female subjects differ significantly in aggressive tendency, thus not corroborating the inference in earlier uncontrolled studies that male papionines are more likely to respond to aggression with counter-attacks or redirection than are females, which instead rely more upon solicitation of aid from third parties (Leonard 1979, Bernstein *et al.* 1983b, Scucchi *et al.* 1988). Such differences have been interpreted as reflecting the greater importance of alliances to females in these species, although any difference in redirection behaviour might equally have been due to the on-average higher rank of males providing a wider range of suitable targets and hence greater opportunity to indulge in such behaviour. Perhaps the disparity in results is due to differences in the methodology employed, or perhaps any sex differences are simply less pronounced in the age group studied here.

Redirection of aggression has been quantitatively demonstrated in immature primates (Anderson & Mason 1974, Aureli & van Schaik 1991a), including species in which the behaviour has not yet been definitively demonstrated in adults (Watts 1995b), and has even been suggested to be more common in immatures than other age classes (Scucchi *et al.* 1988). However, as the latter authors acknowledge, this result may well have been due to the fact that the youngest individuals sampled (in this case predominantly subadults) were more often victims of aggression and thus had more opportunity to redirect. In fact, this response to victimization may only be a viable option if the actor is of sufficient fighting ability and/or rank to ensure that retaliation by the target is unlikely. In general, the rate at which aggression is instigated increases with both age (and consequently size and strength) and rank in juvenile and adolescent cercopithecines (e.g. Caine *et al.* 1983, Bernstein & Ehardt 1985c, Pereira 1988b, Kazem 1993). Unsurprisingly, in the current analysis older immatures also displayed significantly greater redirection tendencies (i.e. post-conflict increases of greater magnitude). Although dominance rank is to some extent dependent upon age in juvenile papionines, particularly among males (e.g.Kuester & Paul 1988, Pereira 1989, 1995, Lee & Johnson

1992; in this population: Kazem 1993, unpublished data), in this case age seemed to exert an independent effect, as a subject's status within its group was not positively associated with the likelihood of initiating post-conflict aggression against bystanders. It seems likely that the reduced availability of suitable (i.e. weaker) targets constrains the ability of the youngest juveniles to mete out aggression without risk of reprisal.

Aggression may be used to gain access to critical resources or to maintain rank, but this would not explain why former victims should be particularly likely to initiate unprovoked attacks in the aftermath of conflicts which, as already mentioned above, would seem to be a relatively risky time to engage in such behaviour. However, it is possible that performance of these acts is intrinsically stress-relieving, thereby reducing the physiological costs of recently having received aggression. This effect might be achieved both because the option of aggression provides the individual with an outlet for "frustration" (see discussion in chapter 4) and because taking positive action allows it to experience some measure of "control" over the social situation - in experimental studies on rodents and primates, both factors have been linked to a reduction in the otherwise elevated glucocorticoid levels usually produced by repeated exposure to physical stressors (e.g. Hanson *et al.* 1976, Davis & Levine 1982; reviewed in Levine *et al.* 1989, Sapolsky 1998). In keeping with this is the observation that, in both dominant and subordinate wild olive baboons, males which often initiated aggression in appropriate situations and which frequently responded to the loss of a fight by redirecting aggression against others had significantly lower basal glucocorticoid concentrations (and a better response to acute challenge) than similarly ranked individuals which did not exhibit these behaviour patterns as frequently (Sapolsky & Ray 1989, Virgin & Sapolsky 1997). An immediate reduction in the physiological stress response generated by the receipt of aggression could explain why the act of redirecting has been associated with a decline in post-conflict rates of self-scratching exhibited by longtailed macaque victims (Aureli & van Schaik 1991b), given that such self-directed behaviour is thought to be an external indicator of the autonomic activation underlying the "fight or flight" response (Maestripieri *et al.* 1992).

However, it is also possible that the rapid decline in scratching documented by the previous authors could in part be due to a reduction in the uncertainty and anxiety which a former victim would usually experience following a conflict. In both this study and that of Aureli & van Schaik (1991b), redirection events were associated with a significant decline in the levels of aggression - thought to be a prime cause of post-conflict anxiety - subsequently received by macaque victims. Although conflicts followed by redirection were on average of lower intensity than those which lacked redirection events this difference was unlikely to account for the result obtained given that, when post-conflict observations in which neither reconciliation nor redirection had taken place were examined, less intense disputes were not in themselves associated with lower levels of received aggression than were more severe incidents. Furthermore, there was no

evidence that the likelihood of being attacked in the period *before* redirection took place (or before the individual average latency to redirection, as applicable) differed systematically between post-conflict observations in which an immature subject did, or did not, redirect aggression. This suggests that the act of redirecting was itself responsible for the observed reduction in aggression received from others, rather than some feature of the preceding conflict influencing both the likelihood of redirection and of receiving aggression. As might be expected, the protective effect of this post-conflict response could only be detected over a relatively short timespan (within the first 3 minutes) following the event, perhaps because its influence wanes as neighbouring individuals move and new ones which had not witnessed the event move into the vicinity. Recent victims are known to be subject to further aggression from both their former opponent and opportunistic bystanders in the aftermath of escalated conflicts (chapter 4; de Waal & Yoshihara 1983, Aureli *et al.* 1989, Aureli & van Schaik 1991b, Aureli 1992, Cords 1992), and it is not known whether the beneficial effect of redirection in reducing such attacks is achieved via an alteration in the behaviour of one or both categories of assailant. However a change in the disposition of the former aggressor, at least, seems likely given that there is some evidence that by responding in this manner a victim can increase the chances that its former opponent will allow a reconciliatory reunion (Aureli & van Schaik 1991a; although again it is difficult to be sure that a causal relationship is involved), which itself has positive consequences in terms of restoring tolerance and reducing subsequent aggression between the protagonists (see discussion in chapter 3).

The fact that redirection events appear to influence the disposition and behaviour of individuals *other than the target* suggests that in post-conflict contexts there is a signalling advantage to be gained by behaving antagonistically, in addition to any benefits which the use of aggression might normally produce (e.g. in terms of resource acquisition, or reinforcement of an existing dominance relationship). In essence, the primary benefit of the behaviour may derive from it being witnessed by third (or rather, fourth) parties. A similar phenomenon has been described by Zahavi (1979), who noted that in nature many aggressive signals transmit far further than actually required for information transfer between the individuals directly involved, suggesting that these signals have been designed to be received by other (more distant) individuals in situations where it pays for the sender to advertise the interaction more widely (see also MacGregor 1993 regarding signalling "networks"). Furthermore, selection is expected to favour adaptations on the part of these extra receivers which allow them to preassess the fighting ability, condition and motivation of potential competitors before becoming involved in any contest themselves; bystanders which derive this information by attending to the outcome of aggression between others can avoid the costs associated with achieving the same via direct experience of an initial contest. There is growing experimental evidence that animals do use "preview" strategies or "eavesdrop" upon contests between conspecifics

and then utilise this information to modify their own behaviour. For example in several vertebrate taxa the subsequent responses of observers, in terms of the latency to aggressive displays and/or the level to which they were willing to escalate, toward individuals seen to win (or lose) a prior dispute were consistent with the witness having identified the former as a relatively strong (or conversely, weak) opponent (red-winged blackbirds: Freeman 1987, domestic chickens: Hogue *et al.* 1996, rainbow trout: Johnsson & Åkerman 1998, Siamese fighting fish: Oliveira *et al.* 1998; see also Naguib & Todt 1997 for analagous experiments in nightingales based upon auditory signals). Similarly, the patterning of agonistic behaviour in the experiments on rhesus macaque triads described above suggested that individuals may "treat others as you have seen them treated" (Mendoza 1993, p. 99).

In the case of redirection, the fact that a former victim is nevertheless still confident enough and capable of threatening or attacking other group members would be useful information for opportunistic bystanders, which might otherwise assume that this would be a good time to take advantage of the actor. In chapter 4 it was suggested that physiological changes prompted by the receipt of aggression, for example a decline in circulating testosterone levels to below some minimum threshold, may place former victims at a competitive disadvantage and/or make such individuals less likely to initiate conflicts (a "loser effect": Chase *et al.* 1994, Hsu & Wolf 1999). If this explanation holds, then the very act of redirecting would seem unlikely to occur. The answer may lie in the fact that victims were significantly more likely to instigate post-conflict attacks against third parties following the receipt of mild as opposed to severe aggression. It is possible that the postulated physiological changes do not occur, or are not of sufficient magnitude to affect the subject's subsequent agonistic behaviour, following low intensity conflicts. Hence, redirection of aggression may be a good indicator that the former victim has not been rendered particularly vulnerable by the preceding incident or does not perceive itself to be so, which should warn bystanders that the former is no less likely to persist and no more likely than usual to be defeated if challenged.

The redirection events observed possessed several features which certainly suggest a potential to draw such acts to the attention of a wider audience. Firstly, redirected attacks were more likely to take place within 5 metres of - and hence often within view of - the perpetrator's former opponent than were equivalent bouts which occurred during control observations, even when initial inter-opponent distance was taken into account. The notion that redirection tends to occur within sight of a former assailant has often been raised in previous studies (e.g. de Waal & Yoshihara 1983, Aureli *et al.* 1992; whereas Watts 1995b provides one report of the opposite tendency), although usually without reference to comparable baseline data. It is not necessary to invoke an intentional basis for this behaviour, nor an ability to understand the viewpoint and knowledge of another individual (available evidence suggesting that monkeys may lack the latter capacity:

Povinelli *et al.* 1991, Byrne 1995, Cheney & Seyfarth 1996, Kummer *et al.* 1996, Heyes 1998); simply by acting quickly a former victim can ensure that its former adversary is still likely to be within the vicinity (the mean interval between the preceding altercation and a redirection event was only 27.5 seconds). However it was not uncommon to observe immature victims glancing back and forth at their previous adversary prior to and whilst threatening their target, sometimes even going so far as to approach and try to enlist the former aggressor. Therefore it is possible that individuals take into account the presence, and perhaps even the orientation and field of view of their former opponent (recent work indicates that rhesus macaques can follow the gaze of conspecifics: Emery *et al.* 1997, Tomasello *et al.* 1998), having learned through experience that redirecting under these conditions is associated with beneficial outcomes. In cases where attempts were made to actively solicit the support of the former opponent the motivation may have had as much to do with inviting cooperation from the latter and thus strengthening the bond between the two, which may itself be a form of reconciliation (de Waal & Yoshihara 1983, Aureli & van Schaik 1991a), as with reducing the chances of renewed aggression from that quarter. At present it is not known whether gaining the former aggressor's support in joint aggression produces the beneficial consequences associated with the more overtly affiliative interactions typically defined as "reconciliations".

Secondly, redirection events disproportionately often incorporated vocal threats, when compared with first bouts of aggression initiated in control observations. Of course, the increased incidence of vocal forms of aggression might simply reflect greater arousal and thus emotional content in animals which have themselves recently been subject to attacks (cf. Dewsbury 1992), but whatever the proximate mechanism the resultant aggression would be more effective at alerting bystanders. As evidence for individual recognition by voice in rhesus is now widespread (e.g. Hansen 1976, Gouzoules *et al.* 84, 1986, Rendall *et al.* 1996; although the extent of individual "signatures" may vary according to call type), the use of vocalizations ensures that the former victim's actions could be identified even by those which could not see the event. However these acts apparently did not force the scapegoat to publicize their receipt of aggression; targets appeared less likely to scream in response to these events than they were when subjected to aggression under baseline conditions, possibly because the aggression received was generally less intense in the former instance. In combination, these results suggest that the protective effect of redirection may derive from making the former victim appear more formidable, rather than by creating a "new" victim and drawing the attention of potentially dangerous onlookers toward this alternative target. Nevertheless, the results presented above concerning the characteristics of the aggression used and its apparent deterrence of subsequent attacks against the perpetrator were based upon a relatively small sample of eligible events, and would therefore benefit from further corroboration.

*Kin-biases in redirection*

There was no evidence for a selective, i.e. disproportionate, increase in attacks by victims against relatives of the former aggressor in the aftermath of conflicts. Such behaviour has been documented in three studies of the genus which utilised mixed-age samples of subjects (pigtail macaques: Judge 1982; longtailed macaques: Aureli & van Schaik 1991a, although not in Aureli 1992; Japanese macaques: Aureli *et al.* 1992, but not in Aureli *et al.* 1993), thus raising the possibility that the failure to demonstrate this phenomenon could be due to its absence in immature individuals. For example, Cheney & Seyfarth (1986) demonstrated that mature vervet monkeys exhibited kin-biases in post-conflict attacks against bystanders and that the relatives of the original protagonists were also more likely to attack each other following a conflict, but found only a nonsignificant trend toward the former and no evidence for the latter more complex form in animals under three years of age (although in a controlled follow-up study on the same population, no mention was made of any age effect in similar results: Cheney & Seyfarth 1989). These authors speculated that the difference might be due to juveniles being less adept at recognizing the social relations which exist between other group members. However, as they acknowledge, it is difficult to specify exactly when such knowledge might be acquired during ontogeny. It is noteworthy that in an early study of captive rhesus monkeys Anderson & Mason (1974) also observed that socially reared juveniles never redirected aggression against targets which were close associates of their former aggressor. In contrast, individuals which had been reared alone often chose targets then regarded as "inappropriate", for example because they were higher-ranking than the actor or related to the aggressor. Thus while the latter result indeed suggests that the abilities to recognize one's own relation to others and the associations between others depends upon social experience (Anderson & Mason 1974, see also Mason 1978), it does not demonstrate that young juveniles lack this social knowledge - in fact the relevant experience might normally be acquired before the end of infancy. Furthermore, the fact that a selective increase in post-conflict affiliation with relatives of a former opponent has been demonstrated in juvenile macaques (chapter 5; Aureli & van Schaik 1991a) and that, in this study, the majority of these initiatives were instigated by the immature subject and did not appear to be simply a consequence of the over-representation of these partners in proximity, suggests that young macaques do possess information on the associates of third parties and are able to utilise this information in post-conflict contexts, at least when choosing individuals with which to affiliate. Rather than lacking either the information or the ability to use that knowledge effectively, young animals might refrain from exhibiting kin-oriented redirection simply because it is not advantageous to do so in the current competitive environment (Harcourt & de Waal 1992). However, the presence or absence of such social knowledge in prepubertal cercopithecines simply has not been rigorously investigated thus far (Tomasello & Call 1997).

Perhaps a more plausible explanation for any difference between immatures and adults is that young individuals are more constrained in their choice of targets for kin-oriented redirection. As Aureli *et al.* (1992) have pointed out, in macaque species in which dominance hierarchies are steep and rigidly enforced recent victims should usually refrain from taking such action. This is due to the risk of counteraggression by the target which, by virtue of the fact that it is related to the former aggressor, is itself likely to outrank the perpetrator (aggressors tend to be dominant to their victims, and related individuals tend to be close in rank), but also because the latter risks provoking intervention by the former aggressor or other high-ranking relatives of the target. As might be expected, kin-biased redirection occurred at very low frequency in the latter study (following only 2.1% of aggressive interactions), and targets were typically young individuals which were subordinate to the redirecting victim. Such attacks were also more likely to occur as part of a polyadic assault on the target, a condition under which the former aggressor would be less likely to intervene in support of its relative. Thus in cases where the former victim is itself a relatively young and low-ranking group member the pool of potential targets will necessarily be much smaller, and few opportunities may arise in which not only are the above conditions met but the former aggressor is also within sight (or earshot) in order to witness the retaliatory event (without which the presumed benefit - a reduction in the likelihood of future aggression from one's former assailant - presumably cannot be derived). Perhaps if analyses concerning immatures had been restricted to only those conflicts with opponents which possessed at least one relative in the group which was younger and/or lower-ranking than both the former aggressor *and* its immature victim, a kin-bias in redirected aggression might have been observed.

Finally, methodological differences between studies may have contributed toward the differences in results obtained. For example, the conditions required for kin-oriented redirection to be a viable option (outlined above) are so specific that it is likely that opportunities to act in this manner are few and far between. This study examined only the first 10 minutes following a conflict, and it is possible that had a longer period of time been examined (e.g. 30 minutes: as in Cheney & Seyfarth 1989, 1 hour: Aureli *et al.* 1992, or 2 hours: Cheney & Seyfarth 1986) a greater number of post-conflict instances might have been recorded. Yet it is worth considering that, as the interval between a conflict and a redirection event increases, it would seem less and less likely that a witness (in this case the former aggressor) would be able to pick out and hence associate these two events from the many other interactions which it has experienced or observed in the interim; a necessary task if the phenomenon is to operate by modifying the aggressor's future behaviour. Secondly, in several quantitative studies (Cheney & Seyfarth 1986, 1989, Aureli *et al.* 1992) post-conflict intervals were compared against "control" periods which had not been matched with respect to time of day; thus we cannot rule out the possibility that an elevation in attacks was demonstrated simply because the animals were

more active and aggressive in those periods during which the initial conflicts (and hence the post-conflict bouts) had been recorded, rather than these conflicts actually having prompted a change in the probability of subsequent aggression. Even where a genuine increase exists, with the exception of one study (Aureli & van Schaik 1991a) there is little evidence that attacks against the opponent's kin are in any way selective, as opposed to merely reflecting a general increase in aggression against all partner types on the part of the former victim (see chapter 5 for further discussion regarding the importance of this check). Additionally, the methods used to demonstrate the selectivity of any post-conflict increase in behaviour themselves vary, with previous studies often comparing the incidence of attacks against relatives of an opponent as a proportion of total aggression against all targets, in post-conflict versus matched-control observations. In this study the preferred index was instead based upon only the first act of aggression per observation, and took baseline levels of the behaviour into account directly for each category of target, because this was felt to be more consistent with the theory underlying and the methods used to demonstrate the original post-conflict increase (which had not been based upon rates of behaviour).

# *General discussion*

*Summary of findings*

Examination of the behaviour of young subjects in the immediate aftermath of conflicts suggested that, in group living taxa, the costs of engaging in aggression with conspecifics extend beyond the physical risks incurred during the encounter itself. Overall, the results were similar to those obtained in previous controlled studies of wild cercopithecines based upon mixed-age subject samples (e.g. Aureli 1992, Castles & Whiten 1998a,b). As might be expected, the role the focal animal had played in the original incident was an important determinant of the extent of any negative sequelae, with former victims bearing the brunt of these costs. In particular, recent victims were likely to receive further attacks, both from their original assailant and from opportunistic bystanders, perhaps because the recipient of preceding aggression is rendered physiologically and psychologically more vulnerable and thus provides an easy target (cf. a "loser effect": Chase *et al.* 1994, Hsu & Wolf 1999). Inspection of post-conflict time budgets revealed that these contestants also spent a lower proportion of time foraging or eating, and a greater proportion in locomotion, compared with baseline conditions - implying that ongoing energetic costs are also incurred. It seems likely that these alterations are due to a need for enhanced vigilance, possibly combined with active avoidance of the former aggressor or other potentially dangerous group members, in the minutes immediately following a conflict. Victims also exhibited a marked elevation in rates of self-scratching, thought to be a behavioural indicator of arousal and/or anxiety (Maestripieri *et al.* 1992), perhaps partly as a consequence of uncertainty about their future treatment by other group members and the risk of receiving further aggression. In contrast former aggressors did not exhibit many of the above patterns of behaviour, although they did display a brief post-conflict increase in rates of self-scratching, despite not being at risk for further aggression. This latter result suggests that the observed changes in self-directed behaviour may in part have been a consequence of either the sympathetic activation provoked by participation in aggression (Castles & Whiten 1998b), or anxiety concerning potential disturbance to the relationship between contestants (Aureli 1997), at least where aggressors were concerned. Finally, both aggressors and victims were more likely to engage in object-directed activities (such as manipulation of stones or twigs) in the aftermath of conflicts, a behaviour which has not been reported in post-conflict work on adult cercopithecines. It is speculated that juveniles, which are more predisposed toward exploratory and object-handling behaviour than adults (see e.g. Huffman 1996, Byrne & Suomi 1996, Mayeaux & Mason 1998), might be particularly likely to engage in such activities when stressed and that their performance might in itself be tension-relieving.

In previous studies friendly reunions between former adversaries have been shown to alleviate a number of these negative consequences, restoring characteristic levels of tolerance, avoidance, aggression and affiliation within a dyad to baseline levels (Cords 1992, Cheney & Seyfarth 1997, Koyama 1997), and probably as a consequence reducing anxiety and uncertainty on the part of contestants and hence levels of self-scratching (in former victims: Aureli & van Schaik 1991b, in aggressors: Das *et al.* 1998). Operationally defined reconciliation was demonstrable in even the youngest cohort of subjects, with the patterning of these events being similar to that documented in previous studies of this species (de Waal & Yoshihara 1983, de Waal 1984, Call *et al.* 1996, Judge *et al.* 1997). For example, disputes which arose over food were significantly less likely to be followed by a friendly reunion than were those with no obvious cause, a difference which has also been observed in several other taxa (e.g. Aureli 1992, Koyama 1997, Castles & Whiten 1998a). This difference was paralleled by one in post-conflict rates of self-scratching, and it seems likely that the proximate cause of both effects is that the greater predictability of aggression which occurs over access to resources provokes a lower degree of anxiety in the participants, which might therefore be less motivated to reconcile. Attributes of the contestants, and the quality of their relationship, were also associated with significant differences in conciliatory tendency. The frequency of reconciliation was higher in conflicts between individuals of similar age than those involving opponents which were more disparate in age. Conflicts between closely related individuals, and between group members known to be close affiliates, were reconciled at higher rates than those between more distantly related individuals or less frequent associates, respectively - differences which have also been documented in several previous studies of macaques (e.g. Aureli *et al.* 1989, Veenema *et al.* 1994, Call *et al.* 1996, Aureli *et al.* 1997). Such variation could be attributed to differences in partner value; reconciliation is expected to be more frequent in relationships of higher value (de Waal 1986b, 1989a; cf. Cords & Thurnheer 1993), for example those between frequent allies such as close kin. In practice, though, relationship value and partner compatibility may covary (Cords & Aureli 1993, Schino *et al.* 1998), and this latter proximate constraint might be a particularly important determinant of reconciliation frequencies where immature individuals are concerned. For example, young subjects might be reluctant to attempt reconciliation with opponents which are much older (hence usually larger and higher-ranking) than themselves, unless they also happen to have a history of nonaggressive social interaction in other contexts (i.e. high compatibility). Finally, rates of post-conflict scratching did not differ significantly according to whether or not the former opponent had been a close associate of the subject, and thus there was no evidence that those relationships presumed to be more valuable were accompanied by a greater degree of post-conflict anxiety on the part of contestants. It is possible that, in immatures, the mismatch between the partners with which an individual reconciles the most (namely close associates) and those which it finds the most valuable is relatively

pronounced. Nevertheless, this result does suggest that not all differences in conciliatory tendency need be mediated by differences in levels of post-conflict anxiety.

The demonstration of post-conflict increases in affiliation with partners *other than* the opponent were perhaps more surprising, given that studies of macaques - particularly those considering the victims of aggression - have often produced little evidence for such behaviour. For example, following polyadic conflicts there was a pronounced increase in affiliative contacts between former coalition partners (an effect also reported by de Waal & Yoshihara 1983, Castles & Whiten 1998a), these overtures typically being instigated by the beneficiary of the support. It is possible that contestants seek proximity and interaction with individuals from which they have recently received agonistic aid as a means of reducing the risk of receiving either renewed attacks from their original adversary or opportunistic aggression from bystanders. Alternatively, interactions involving grooming might provide young animals with a means of "thanking" their allies for services rendered, and thus encourage the provision of future support (cf. Hemelrijk 1994). However, it is not yet known whether these interactions took place predominantly because coalition partners tended to be maternal kin (or at least close associates), or specifically because of the support these individuals donated. It was notable that immature subjects also engaged in affiliation with previously uninvolved bystanders at elevated rates in the wake of conflicts, these interactions being disproportionately directed toward their own maternal relatives or those of their former adversary. Young primates have been reported to seek the company of close kin following involvement in aggressive confrontations (e.g. Pereira 1993, Watts 1995b, Weaver & de Waal, in press), perhaps for reassurance and/or protection from subsequent harassment, although a selective increase in affiliation with related bystanders has only been documented in a minority of those studies using mixed-age samples (Judge 1991, Petit & Thierry 1994). The degree to which kinship influenced the likelihood of post-conflict interaction was affected by sex; only in female subjects was affiliation disproportionately directed toward their own relatives. This apparently reduced importance of kin bonds to immature males (and conversely, of males to their kin) echoed that seen in reunions between former opponents, with females being more likely to reconcile with closely related opponents as opposed to other adversaries, whilst no such distinction was apparent in male subjects. In both cases, patterns of post-conflict behaviour seem to reflect sex differences in the extent to which maternal kin are represented among an individual's closest associates (females being more kin-biased than males), as might be expected given the sex-specific life history trajectories of macaques. Otherwise, there were no marked differences between the sexes in post-conflict behaviour; for example both male and female contestants exhibited a selective post-conflict increase in affiliation with the relatives of former adversaries. These interactions were not simply a side-effect of reconciliation between the opponents themselves nor of

differential proximity to specific classes of group member, instead being consistent with the interpretation that individuals selected social partners on the basis of knowledge of the bonds existing between third parties (see e.g. Dasser 1988a, Cheney & Seyfarth 1999). The tendency to affiliate with relatives of former opponents was negatively associated with contestant age; similarly, in a study of longtailed macaques (Aureli & van Schaik 1991a) it was only in juvenile subjects that this pattern could be demonstrated, and not in the entire mixed-age sample. Such peaceful overtures have been hypothesised to prevent conflicts subsequently spreading to encompass other members of the protagonists' matrilines (Judge 1991, Das *et al.* 1997), or somehow to "substitute" for reconciliation with the opponent itself (Cheney & Seyfarth 1989, Aureli & van Schaik 1991a) in cases where the latter appears unapproachable or is otherwise occupied, although both functions remain to be tested.

Finally, the negative ramifications of intragroup conflicts often extended beyond the original adversaries; both aggressors and victims were more likely to threaten or attack previously uninvolved third parties under post-conflict conditions, and this risk appeared especially marked for the relatives of former victims. Attacks by former aggressors against bystanders, as opposed to renewed hostilities toward the initial opponent, have not previously been demonstrated in controlled post-conflict work (see e.g. Das & van Hooff, in press). It is suggested that it may be cost-effective to instigate further attacks once already physiologically prepared for aggression, especially if individuals are more likely than usual to win successive confrontations (a "winner effect": cf. Chase *et al.* 1994). Furthermore, sequential assaults directed against close relatives of the victim may allow an aggressor to reinforce its rank position over the entire family, in a situation in which it possesses enhanced information regarding their likelihood of supporting one another. However, subjects were significantly more likely to aggress against third parties when they had been the victim, rather than the instigator, of the original conflict ("redirection": Anderson & Mason 1974, Scucchi *et al.* 1988, Aureli & van Schaik 1991a). Whilst performance of such acts might be intrinsically stress-relieving, they may also constitute an honest signal of the perpetrator's physiological condition and confidence, thereby preempting the harassment from former opponents or opportunistic bystanders to which recent victims are often subjected. Redirection of aggression was more likely to occur following low intensity conflicts, and was associated with a significant decline in the levels of aggression subsequently received by former victims (see also Aureli & van Schaik 1991b). Redirection events were also more likely to occur within 5 metres (and hence within sight) of former opponents, and to utilise vocal threats, than were baseline bouts of aggression by the same individual, thus potentially allowing the perpetrator's actions to be brought to the attention of a wider audience. Neither sex nor rank exerted any appreciable effect upon initiation of post-conflict aggression. However older immatures were significantly more likely to redirect threats and attacks

after being victimised (i.e. exhibited post-conflict increases of greater magnitude), suggesting that reduced availability of suitable (smaller, weaker) targets may constrain the ability of youngsters to respond in this manner without risk of reprisal from the target or its supporters. There was no indication of redirection being disproportionately directed toward relatives of the former aggressor, as has been reported in a minority of studies utilising mixed-age macaque samples (Judge 1982, Aureli & van Schaik 1991a, Aureli *et al.* 1992). Again, this might reflect lack of opportunity amongst immature victims (lower probability that an even younger and hence more vulnerable relative of the opponent is available as a target), although methodological differences between studies are also likely to have contributed to the difference in outcome.

*Suggested extensions*

This study therefore suggests that immature macaques possess a rich repertoire of post-conflict behaviour, and there appears little reason to believe that young animals are any less accomplished in this respect than adults are reported to be. However, these results remain only a first step toward establishing the capabilities of young rhesus. Firstly, caution needs to be exercised because the data are only correlational and hence associations found between specific variables and the occurrence of particular post-conflict behaviours should not be over-interpreted (Milinski 1997); experiments are now required in order to confirm some of the postulated causal connections. Given that the basic patterns of behaviour exhibited in the aftermath of aggression now seem relatively well established in cercopithecines, it might be useful to first concentrate upon possible relationships between alternative responses, in order to better understand the social decisions which former contestants may face. For example, there is some indication that affiliation between former coalition partners might exert an inhibitory effect upon the likelihood that reconciliation between adversaries would be attempted. Although conciliatory tendencies did not differ significantly between dyadic and polyadic conflicts overall (see chapter 3), when the comparison was restricted to only those polyadic disputes in which the subject had received agonistic support the latter proved to be reconciled at significantly lower rates ($p = 0.002$). Of course, there may have been systematic differences between the two types of conflict, and a causal connection cannot be assumed, but it is nevertheless possible that affirming the bond with an individual which has just proved itself willing to support one takes precedence over preserving a relationship in which a conflict has just occurred. In a similar vein, we might ask whether reconciliation with a former adversary is usually the primary concern, such that contact with one's own kin or that of the opponent is attempted only when a reunion with the opponent itself seems unlikely (e.g. if the victim is inhibited from approaching an aggressor much larger and/or higher-ranking than itself, in cases where the two do not happen to be close associates), or whether the reverse priority holds. In this respect it is

interesting to note that work on immature capuchins has suggested that the quality of the mother-offspring bond may determine whether a young victim initiates rapprochement with an adult foe, with more secure youngsters preferentially seeking contact with their mothers whilst those with insecure bonds instead directed overtures toward their former opponent (Weaver & de Waal, in press).

A related issue, and one where experiments might prove particularly useful, is to look at the implications of these choices. With the exception of work concerning reconciliation between former opponents (e.g. Aureli & van Schaik 1991b, Cords 1992, Silk *et al.* 1996, Koyama 1997), there is very little hard evidence regarding the functional consequences of the social interactions which take place in the wake of aggression; in essence, many hypotheses have remained as mere speculation for more than a decade. Examples highlighted in this thesis include the issue of whether affiliative overtures toward a former coalition partner by the beneficiary of support constitute some kind of "payment" for services rendered, and whether these conspicuous reunions might be effective in reducing the levels of subsequent aggression directed against the participants. Likewise, in order to understand the reasons for post-conflict affiliation between contestants and relatives of their former opponents we first need to establish whether the former are actually at risk of attacks from the latter (or *vice versa*) and if so, whether affiliative exchanges are associated with a reduction in the likelihood of receiving aggression from the particular family member involved. On the other hand, if these interactions are proposed to "substitute" for reconciliation with the adversary itself (cf. Cheney & Seyfarth 1989, Judge 1991), it is important to know whether and what aspects of the behaviour of the opponent might thereby be affected. At present, only one study - on longtailed macaque aggressors - has attempted to critically examine the short-term effects of interacting with third parties in the aftermath of conflicts (Das *et al.* 1998, Das & van Hooff, in press), providing a salutory warning in that there appeared to be little support for current predictions concerning the outcome of affinitive exchanges between these contestants and their opponent's kin or unrelated bystanders. A further, and related, theme to emerge from this thesis concerns the extent to which post-conflict interactions may influence, and may even be designed to influence, the behaviour of individuals *other* than the immediate participants. To date, consideration of the role of signalling in post-conflict behaviour has generally focused upon the individuals directly involved; for example in considering whether the use of explicit gestures usually confined to the post-conflict context serves to clearly indicate the cessation of hostilities to the receiver (e.g. the hold-bottom ritual of stumptail macaques, and the loud squeals which often accompany reconciliation: de Waal & Ren 1988, de Waal 1989b), or whether affiliative gestures towards former adversaries might constitute reliable indicators of the actor's currently benign intent (Silk 1997). Yet a number of commonly proposed consequences of post-conflict behaviours implicitly assume that there must be effects

upon the disposition and future actions of additional witnesses. For instance, if redirection of aggression against bystanders actually increases the likelihood that a reconciliatory reunion is subsequently granted by the previous aggressor (Aureli & van Schaik 1991a), the latter must have attended to the aggression displayed by its former opponent and modified its behaviour accordingly. Thus consideration of the extent to which the presence, identity and actions of third parties may influence the course of post-conflict events is an area of investigation which might prove fruitful.

Finally, the post-conflict responses detailed above comprise only one aspect of conflict management in primates (see chapter 1), many of which have not yet been systematically investigated in immature individuals. For example, analyses of complex multipartite agonistic interactions, thought to involve decisions which take into account the identity and likelihood of intervention of potential allies of both factions as well as the use of appropriately directed recruitment behaviour (cf. Kummer 1988, Harcourt 1988, 1992, Silk 1992a, 1999), have infrequently focused upon immature contestants. It has often been assumed that weanlings lack the underlying social knowledge (for example regarding the relative ranks and habitual associates of third parties) needed in order to behave effectively, and that these (and other) social skills are acquired during the prolonged prereproductive period so characteristic of the primate order (e.g. Cheney & Seyfarth 1986, Joffe 1997), although in fact there is little relevant behavioural evidence one way or the other. Whilst communicative competence relevant to agonistic interactions (e.g. the production of recruitment vocalizations which accurately label the relative rank and relatedness of an assailant: Gouzoules 1989, 1995) is known to improve in proficiency over the juvenile period in macaques, direct evidence that the failings of younger animals are due to a more basic deficit in social knowledge is absent. Indeed, there are some hints that immature individuals are both aware of and adept at utilising information on triadic relations, for example regarding kinship between their opponents and third parties (chapter 5; Aureli & van Schaik 1991a). An alternative viewpoint would suggest that young cercopithecines are under pressure to acquire an extensive knowledge of their social network relatively early in the lifespan - for instance before the end of infancy, a period in which they are to some extent still buffered by their mothers against environmental and foraging demands, but during which their increasing independence already exposes them to high levels of aggression from other group members. In this view, juveniles may refrain from acting in ways which would demonstrate the extent of their social understanding simply because it is not advantageous to do so at that life stage ( e.g. due to the limitations of low physical strength or rank; Harcourt & de Waal 1992). The task of documenting age-related changes in social knowledge is likely to be additionally complicated by the need to ensure equivalence of task demands in comparisons between cohorts (e.g. with respect to memory demands, or the level of motor coordination required). Perhaps the "looking time" paradigm long used in work

on pre-verbal human infants and recently pioneered to examine aspects of physical cognition in (adult) nonhuman primates (Hauser & Carey 1998), or the playback experiments devised to explore knowledge of rank and kin relations between other individuals in adult baboons (e.g. Cheney *et al.* 1995a, Cheney & Seyfarth 1999), are techniques which could now be extended to document the knowledge and abilities of immatures. These protocols have the additional advantage that extensive periods of training are not required (a potential difficulty if the work aims to examine abilities at an age when they may be changing rapidly), and furthermore can be applied to ecologically relevant tasks in the field. Such work would do more than merely contribute to our understanding of conflict management in primates; outlining precisely which skills remain to be perfected during the juvenile life phase would have implications for theories concerning the evolution of delayed reproduction in primates, whilst it has long been acknowledged that examination of the "building blocks" of cognition via the ontogenetic route is often a good way of more fully understanding the adult endpoint achieved.

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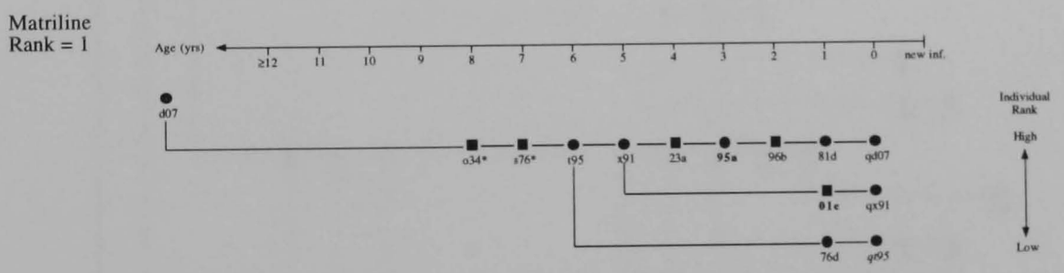
# *Appendix A1*

## *Matrilineal relationships within groups R and BB*

Vertical connections denote mother-offspring groups; horizontal connections denote siblings, presented in birth order. Matrilines are presented in rank order, with the highest ranking (1) placed first. Within matrilines and families, rank of mothers and their offspring decreases down the page. Adult and subadult male immigrants are included only if other members of their family had also transferred into the same group (although the transfers did not occur together); otherwise all non-natal male group members are listed in Appendix A2.

### *Group R*



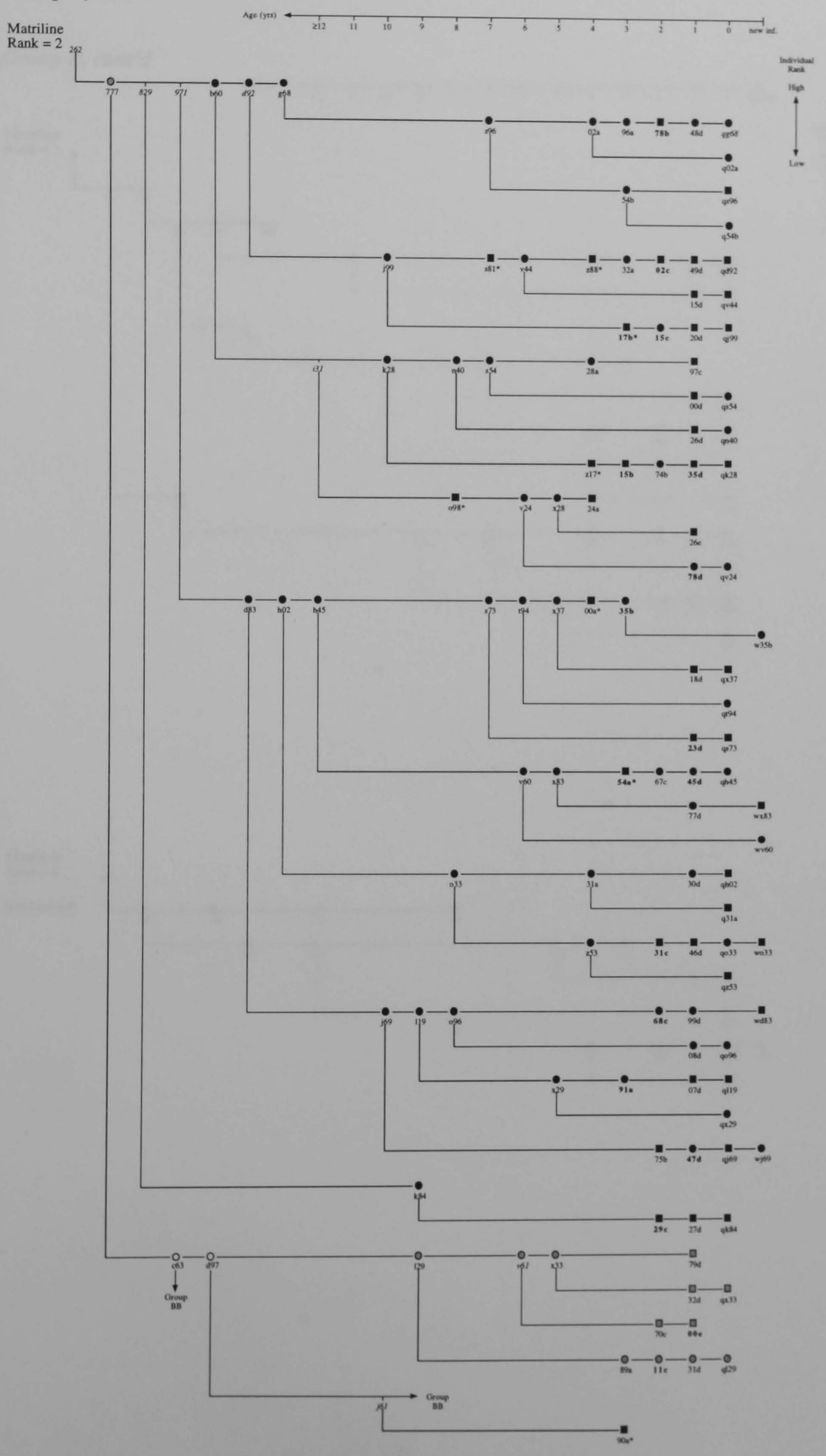

Actual rank of c12 + family

Actual rank of k84 + offspring

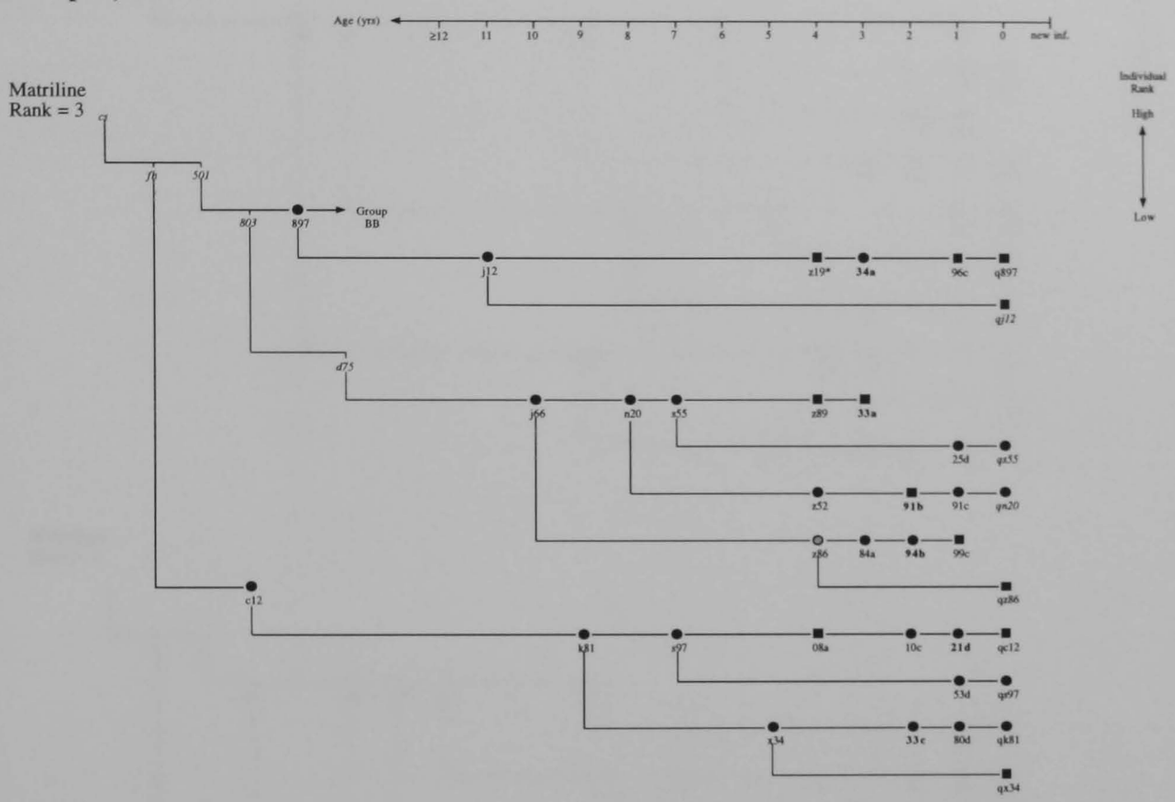
***Key***

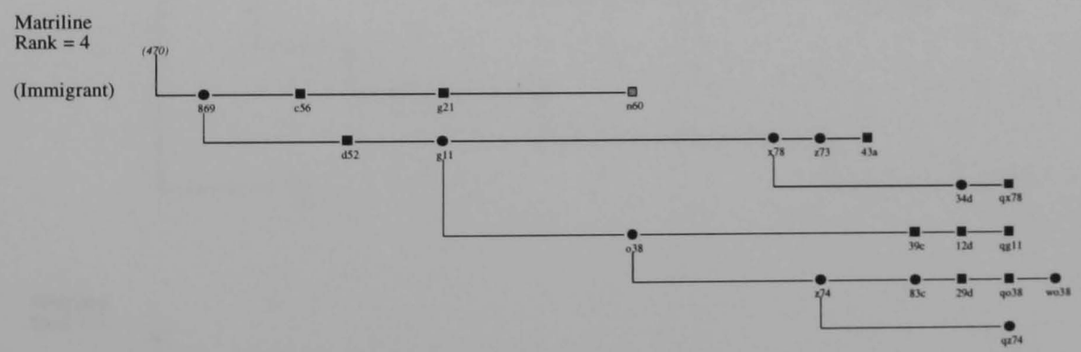
| | | | |
|---|---|---|---|
| ■ | Male | **bold** | Focal juvenile |
| ● | Female | * | Temporary male resident |
| ■ | Natal resident group R | *italic* | Individual died during study |
| □ | Natal resident group BB | ( ) | Linking female; never member of group |
| ▨ | Transferred between R and BB | (*italic*) | As above; died before study |

## *Group R, cont'd*

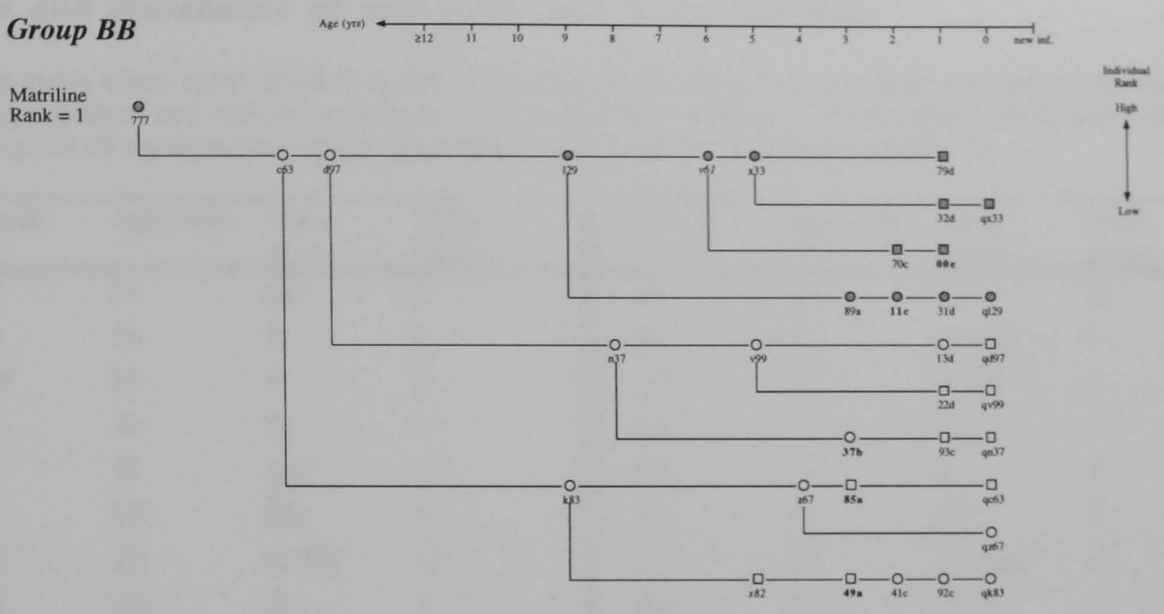


## *Group R, cont'd*



## *Group BB*


Age (yrs)
≥12
11
10
9
8
7
6
5
4
3
2
1
0
new inf.
Individual Rank
High
Low
Matriline Rank = 1
777
c53
d77
129
v51
x33
79d
32d
qx33
70c
00e
89a
11c
31d
ql29
n37
v99
13d
qd97
22d
qv99
37b
93c
qn37
k83
z67
85a
qc63
qz67
z82
49a
41c
92c
qk83
Matriline Rank = 2
c
f1
301
803
b10
e55
g17
k89
24d
qk89
s18*
z93
90b
75d
qg17
o27
86a
93b
16d
qe55
25b
14d
qo27
j01
k79
n41
93a
17d
qb10
02e
qn41
x79*
36b
95b
51d
52a
32c
qj01
d75
(j66)
z86
qz86
c55*
Matriline Rank = 3
(Immigrant)
(470)
(678)
(869)
(156)
n60
t53
(g11)
t54
z76*
(g80)
(137)
94a
84c
06d

# *Appendix A2*

## *Age and provenance of non-natal male group members*

Only males which spent ≥25% (9 weeks) of the main study period within a group are counted as *resident* group members and utilised in analyses. All others listed transferred into the group for ≥2 consecutive weeks but <9 weeks in total, and are classified as only *transient* individuals (marked †).

| ID code | Age/ years | Study group | Natal group | ID code | Age/ years | Study group | Natal group |
|---|---|---|---|---|---|---|---|
| 632 | 21 | BB† | I | i37 | 11 | R | Q |
| 708 | 20 | R | L | i64 | 11 | R†, BB | F |
| 722[d] | 20 | R | L | i78 | 11 | R, BB | L |
| 761 | 20 | R | J | j19 | 11 | R | L |
| 833 | 19 | BB† | O | j47 | 11 | R | F |
| 856 | 19 | BB | J | j86 | 10 | BB | F |
| 912 | 18 | R, BB | O | k14 | 10 | R†, BB† | L |
| 933 | 18 | R | F | k27 | 10 | R, BB | L |
| 978 | 17 | R†, BB | F | k57 | 10 | R | Q |
| 983 | 17 | R, BB | F | k85 | 9 | R | S |
| a48 | 17 | R | F | l01 | 9 | BB† | Q |
| b71 | 16 | R, BB | I | l32 | 9 | R | F |
| c18 | 16 | R | I | n60* | 8 | R, BB | S |
| c56* | 15 | R | I | o15 | 8 | R, BB | F |
| c61 | 15 | R, BB | I | o19 | 8 | R†, BB† | F |
| c78 | 15 | R, BB | L | o23 | 8 | R, BB | F |
| c98[d] | 15 | R† | I | o49 | 8 | R | F |
| c99 | 15 | R | I | s47 | 7 | R† | F |
| d38 | 15 | R, BB | I | s60 | 7 | R | F |
| d52* | 15 | R | I | t29 | 6 | BB† | F |
| d71 | 15 | R | I | t30 | 6 | R | F |
| e05 | 14 | BB† | I | t53* | 6 | BB | S |
| e54 | 14 | R†, BB | I | t54* | 6 | BB | S |
| f26 | 14 | R | F | t71 | 6 | R | F |
| f27 | 14 | R | F | t88 | 6 | R | F |
| f32 | 14 | R, BB† | I | v29 | 6 | R†, BB† | L |
| g07 | 13 | R†, BB | I | v45 | 6 | R | F |
| g09 | 13 | R | I | v59 | 6 | R | F |
| g13 | 13 | BB† | I | v83 | 5 | R†, BB† | F |
| g21* | 13 | R | I | v92 | 5 | BB | F |
| g62 | 13 | R, BB | L | x48 | 5 | R† | F |
| h47[d] | 12 | R | I | z76* | 4 | BB | S |
| h90 | 12 | R, BB† | I | 17a | 4 | R | F |
| h91 | 12 | R, BB | F | 60a | 3 | R | F |
| i06 | 12 | BB | F | 21b | 3 | R | F |
| i30 | 12 | R | F | | | | |

[d]Individuals which died during the study period. *Males related to the immigrant matriline from group S (and hence listed in the matriline in Appendix A1), but which had transferred in independently. Groups Q, R, and S all fissioned from group I in the mid-1980's, thus there is a possibility that males born in the years immediately following these fissions may be relatively closely related to some older individuals from these other groups.

# *Appendix B*

## *Behavioural definitions*

The following behaviour patterns were continuously recorded during focal and PC/MC observations. Duration of all behaviour patterns marked (†) was timed to the nearest second, any which lasted <5 seconds being noted as either a "brief" contact behaviour (those terminated by the actor) or a behaviour "attempt" (those terminated by the recipient). All other behaviours were scored as bouts of undefined duration. Repetition of most behaviours was scored as a new bout if [a] ≥10 seconds had elapsed between occurrences, or [b] the subject had switched to a mutually exclusive activity or, for contact behaviours, [c] one or both partners had broken contact and moved beyond arm's reach (0.6m). The only exceptions were self-directed behaviours (a new event being scored if ≥5 seconds had elapsed or the subject switched to another class of self-directed behaviour), and aggressive events (in which a number of different agonistic patterns might occur in quick succession, those occurring within <30 seconds of each other being treated as one bout, unless one or both opponents had switched to a mutually exclusive category of behaviour in the interim).

Interactions with mother-infant pairs (where the infant was suckling, or being held or carried by the mother) were scored as interactions with the mother only, unless the act was specifically directed toward or initiated by the infant. Where the identity of an extragroup partner was not known, the interactant was simply categorised by age-sex class and group (where possible).

## *Affiliative interactions*

*Contact*† Resting in physical contact with another individual. Gentle touching or patting, whereby the hand (commonly of an approaching animal) is extended to touch face, shoulders or hindquarters of another individual was scored as "brief" contact.

*Brush past* Transitory and non-agonistic contact as one individual passes by another; the recipient may be either stationary or walking.

*Groom*† Picking through fur or over the skin of another individual, using hands and/or mouth. This behaviour was not scored unless a minimum duration of ≥5 seconds was achieved.

*Mutual groom*† Simultaneous grooming of each other by two individuals; may occur wholly embedded within or partially overlapping with a bout of unidirectional *grooming* between the same partners. This behaviour was not scored unless a minimum duration of ≥5 seconds was achieved.

*Groom solicit* Inviting another to groom by presenting a body part (e.g. shoulder or flank) to the partner often with the face simultaneously turned away, by lying down in front of the partner, or by adopting a characteristic version of the *present* posture with a confident stance and tail typically held straight up.

*Groom pull* Encouraging grooming from another individual by tugging at the latter, often at its forehead or arm, and positioning self directly in front of the recipient. Generally used by adult males, and can be an assertive gesture.

*Embrace*† Resting with arms wrapped around a partner. Ventral (hence reciprocal) embraces and dorsal hugs were distinguished.

*Arm round*† Approaching and placing one arm around the shoulders of a stationary or walking partner (in latter case, the actor continues to move alongside the partner). Characteristic of juveniles, especially males, and used both in affiliative contexts and to *passively support* another youngster during an aggressive interaction.

*Carry*† Transporting of a younger individual, almost invariably an infant or yearling. The beneficiary's position, either clinging to the actor's ventrum or riding dorsally, was specified. Retrieval and gathering up of the recipient into a carry might also be prompted by the proximity or actions of a third party.

*Carry invite* Encouraging a younger individual to ride dorsally upon the actor, by orienting towards the latter at close range and pausing whilst lowering shoulder towards the ground, usually also glancing (or even vocalizing) at the intended partner.

*Carry start* Initiation of a dorsal or ventral *carry* by the beneficiary, usually by approaching and jumping onto an older individual's back or haunches.

*Infant affiliate*† Friendly handling of, or by, an infant (or occasionally yearling), including holding, nuzzling, or clambering upon the partner, but without the more boisterous gestures characteristic of *social play*.

*Social play*† Interaction using motor patterns often observed in other functional contexts, but during relaxed circumstances and characterized by exaggeration and repetition of movements, lack of ritualized agonistic signals, inhibition of aggressive movements, and frequent reversing of roles. Occasionally incorporating elements of *object play*, such as gentle tug-of-war games over grass stems or branches, and chasing games involving the loss and repossession of objects such as flower buds or coconut husks. Most frequently seen between immatures, but also occurs between adult and immature males, or between young adult females and infants. Occurrence and sequence of the following two intergrading types of play were scored within each bout:

*Play chase* Approach-withdrawal play, incorporating mutual leaping toward/over the partner with or without brief contacts, relaxed pursuits, hide-and-seek motions around objects, dive-bombing individuals swimming in water pools, and arboreal dangling and swinging if oriented toward a similarly engaged partner.

*Play fight* Rough-and-tumble play typified by whole-body wrestling, or rearing and grappling whilst mouthing and mock-biting the partner; also stationary pawing or holding of a partner while engaging in prolonged and restrained mouth-to-mouth contact.

*Play invite* Encouraging another to play by gambolling past the latter whilst glancing back over the shoulder (sometimes also dragging a branch or other object, or holding it in the mouth and shaking the head from side-to-side), adopting a play-present posture with hindquarters elevated and head and shoulders lowered to ground, or by brow-lifting. The latter signal was especially used by young males, involving retracting the scalp and brow several times in quick succession, sometimes incorporating eyelid flashing, and with the mouth in relaxed position.

*Play initiate* Starting a play bout by approaching and contacting the intended partner, either by pulling the partner toward oneself or by patting the latter whilst bounding past.

*Play face* Relaxed open mouth display, sometimes accompanied by soft low panting vocalizations. Used to indicate playful intent, particularly at the start and during interruptions of play bouts.

*Nuzzle*† To gently rub one's face back and forth against the face of another individual. Duration was only recorded if the interaction lasted ≥5 seconds.

*Smell*† Brief muzzle-to-muzzle contact, often - although not exclusively - when recipient had been foraging, or placing of nose against the shoulder or flank of recipient. Again, not scored as affiliative if actor's demeanour was suggestive of assertive or intimidatory intent. Duration was only recorded if the interaction lasted ≥5 seconds.

*Mount (affiliative)*† Placing hands on hips or waist of another individual and mounting or climbing upon the latter in a pseudocopulatory fashion. Particularly frequent among young males, which use mounts as a greeting, to start play bouts, and during *passive support* of another individual engaged in an aggressive interaction. Duration was only recorded if the mount lasted ≥5 seconds. Not counted as affiliative if actor's demeanour suggested the mount was predominantly assertive, or sexual.

*Tail wag* Rapid and vigorous side-to-side movement of the tail, and in extreme cases the haunches, performed either when standing or seated. Often accompanied by a mixture of *girneys* and/or excited squealing. Almost exclusively exhibited by infants and young juveniles, when attempting to initiate, or in response to the receipt of, a positive overture.

*Lipsmack* Facial expression produced by protruding and rapidly moving the lips up and down, without opening the mouth. Accompanied by audible lip- and tongue-smacking. An affiliative or distance-

reducing display, most often given during initiation or maintenance of peaceful contact, and often responded to in kind. Also produced in contexts involving apparent reassurance, when enlisting third parties during an ongoing dispute, or as a sexual invitation to a consort partner.

*Girney* Soft, low-pitched, quavering and rather nasal vocalization, which may be given in a long series and responded to in kind by the addressee. Accompanied by pouted but minimally separated lips, which are vigorously moved up and down as if chewing. Uttered at close range, during the initiation and maintenance of affiliative interactions.

*Low grunt* Low amplitude, pulsed, hoarse and breathy call, directed toward another individual at close range. Often emitted two or three times in quick succession, and typically given as one individual approaches or is approached by another, or in response to shifts in position or changes in the behaviour of an associate. Appear to promote subsequent affinitive interactions, and may be responded to in kind.

*Short coo* Soft clear sounding and relatively high pitched call, similar to a very brief version of the *whoo* call, and directed to an individual in close proximity. Produced when approaching and initiating an affiliative interaction, or in response to the movements of a social partner. Typically used by immature individuals, but a similar call was occasionally given by adult females to their younger relatives. Coos seem very variable, and a subtype termed *rising coo* was distinguished in young individuals, characterized by a rapid dip and then rise in pitch or the reverse inflection. Both types often provoked a response from other immatures, whether in kind or involving *girneys* or *grunts*.

## *Agonistic interactions: aggressive*

Aggressive behaviour patterns are presented here in order of decreasing intensity, with higher acts often used in conjunction with less severe gestures such as threats. Therefore in prolonged bouts only the sequence of major high intensity acts was noted. Additionally, the term *fight* was used as a shorthand to describe relatively prolonged incidents involving bidirectional *grabbing* and/or *biting*. Where either of the initial contestants were using or had been within 0.6m of a resource (e.g. water, chow, forage, soil spot) the latter would be specified, as would the outcome (whether the resource was retained, transferred, relinquished but then ignored by the victor, or co-utilised). In cases where the recipient of aggression had been in contact affiliation with a third party and the aggressor caused one member of the dyad to break contact with and/or leave the other, this would be specified as either a *disrupt transfer* (where the aggressor then established contact with the third party within ≤5 seconds) or a *disrupt separate* (where the aggressor did not immediately establish contact with the third party, merely having separated the initial dyad). In cases where the aggression was clearly directed toward gaining access to a social partner, but was unsuccessful in separating the initial dyad, this would be recorded as a *disrupt attempt*. Similar qualifications were utilised with respect to the acts defined as assertive (see section below).

*Fierce bite* Sustained and/or repeated bites lasting ≥5 seconds, often involving head-shaking or slashing with the canines and typically performed whilst pinning down the victim, which often result in injury to the recipient.

*Bite* Single bite, with or without holding down of recipient.

*Grab* Aggressive manual contact, likely to cause discomfort but not actual tearing of the victim's skin. May occur singly, and may or may not culminate in pinning down the recipient.

*Grab at* Swiping gestures in which the actor attempts to grasp an opponent, but fails to make contact.

*Chase* Running pursuit or charges toward another individual for a distance of ≥2 metres, generally following a recipient which *flees*.

*Lunge* Rapid aggressive movement toward another individual, covering a distance of <2m. Usually accompanied by facial and/or vocal *threats*.

*Push* Manual contact predominantly aimed at moving the recipient out of the way, occurring as single gestures and lacking the intensity of a *grab*. Includes slapping and pulling at the recipient and, unlike the acts described above, is typically not accompanied by other threatening gestures.

*Vocal threat* Hoarse, low-pitched pulsed call, produced with rounded and protruded lips. Often directed toward an opponent several times in quick succession and accompanied by aggressive staring and posture. May vary in intensity from low panting grunts to louder harsh barks.

*Male threat* Visual threats involving very pronounced brow-raising and dipping of the head (see *facial threat*, below), accompanied by stylised prowling movement toward the target which is usually situated at some distance. Only observed in males, including older juveniles, and often followed up by more direct aggressive action if the target is either unaware or has not immediately responded with a submissive gesture.

*Facial threat* Fixed staring clearly directed towards another individual, often at close quarters, accompanied by one or more of the following: head-bobbing, brow-raising with ears flattened back, opening the mouth as if to produce a *vocal threat*, or slapping the ground with one hand.

*Stare threat* Mild version of the *facial threat*, involving a clear stare directed at the recipient in an intimidatory fashion, but lacking the other components.

## *Agonistic interactions: assertive*

*Neck chew* To briefly nip the back of another individual's neck whilst passing past, usually as part of an *encircling* movement (see below). Only performed by adult or occasionally subadult males, and almost invariably directed toward another mature male.

*Encircle* Approaching and slowly circling around another individual in an intimidating manner, passing close enough to brush against the recipient's fur. May culminate in a *neck chew*, before the actor continues on its way. Again, only performed by adult or occasionally subadult males, and almost invariably directed toward another mature male.

*Rough behaviour*† Manual contact likely to cause discomfort to another individual, for example dragging an infant along the ground, but without sharp movements such as *grabbing* or obvious aggressive intent on the part of the actor. Duration was only recorded if the interaction lasted ≥5 seconds.

*Take resource* To prise a forage item or piece of chow from the hands or feet of the reluctant, but generally acquiescent, current owner.

*Cheek inspect*† To manually and/or visually inspect the cheek pouches of another individual. Usually, but not always, accompanied by removal of the contents (*take resource*, above). Duration was only recorded if the interaction lasted ≥5 seconds.

*Take partner* Physically dragging or carrying away the partner (usually an infant or young juvenile) with which another individual was interacting affiliatively, in order to interact with the third party oneself.

## *Agonistic interactions: approach-retreat*

*Supplant* An approach directed toward another individual, which irrespective of whether performed assertively results in the latter moving away within ≤5 seconds, thereby relinquishing a spatial position or resource. Supplants in which the recipient withdrew as the actor approached to within ≤2m, or only when the latter had approached to within arm's reach (≤0.6m) were distinguished. Where the recipient was using or had been within 0.6m of a resource (e.g. water, chow, forage, soil spot) the latter would be specified, as would the outcome (whether the resource was retained, transferred, relinquished but then ignored by the supplanting individual, or co-utilised). In cases where the recipient had been in contact affiliation with a third party and the supplant caused one member of the dyad to break contact with and/or leave the other, the supplant would be specified as either a ***disrupt transfer*** (where the supplanting individual then established contact with the third party within ≤5 seconds) or a ***disrupt separate*** (where the supplanting individual did not immediately establish contact with the third party, merely having separated the initial dyad).

***Passing supplant*** Apparently non-aggressive movement which resulted in the withdrawal of another individual from one's path at a distance of ≤2m; distinguished from a ***supplant*** by the fact that the actor's motion did not appear specifically directed toward the recipient but was instead simply passing past the

latter. Again, whether the recipient withdrew as the actor moved to within ≤2m, or only when the latter had moved to within arm's reach (≤0.6m) would be distinguished. Where the recipient was using or had been within 0.6m of a resource (e.g. water, chow, forage, soil spot) the latter would be specified, as would the outcome (whether the resource was retained or abandoned).

*Avoid* Withdrawal from an apparently unaggressive individual which was potentially approaching or walking past the actor, at a distance of >2m (their separation at the time being specified in metres).

## *Agonistic interactions: submissive*

*Cower* Leaning away from another individual with hunched and tense posture and gaze lowered, or freezing by crouching to the ground with limbs bent and spine flexed dorsally. Usually in response to an approach, or aggression, by another animal.

*Grimace* Facial display in which the lips are retracted so that clenched teeth are exposed. Given in response to the actions of another animal, and appears to formally signal submission by the actor.

*Waver* A clear sounding, high pitched, prolonged and undulating scream, which conveys less sense of urgency than the *scream* described below. Lip retraction and other indicators of fear are reduced in comparison with those accompanying a *scream*. Sometimes produced in response to the receipt of relatively minor aggression, but in immatures is often unprovoked and directed at more powerful targets in an apparent attempt to incite other group members to aggress on behalf of the actor; in general appears to function to recruit support.

*Squeal* Brief, clear sounding and less intense version of a *scream*, usually given by immatures in response to threats or other mild aggression, or to unwanted rough behaviour.

*Scream* Loud, high pitched, often harsh sounding calls of prolonged duration, given when threatened with or receiving aggression. Accompanied by retraction of the lips, with the teeth parted. Several types of scream have been identified in rhesus (e.g. noisy, pulsed, tonal), apparently corresponding to the severity of the aggression received, and the degree of relatedness and relative rank of the opponent.

*Flee* Rapid withdrawal (running or climbing) from another individual, either spontaneously or in response to the threat or receipt of aggression.

## *Agonistic interactions: third party events*

*Enlist* Repeated gestures toward a previously uninvolved bystander in order to request agonistic support in an imminent or ongoing aggressive confrontation. Most pronounced form involves headflagging by alternately looking back and forth from the solicited individual to the opponent, often whilst threatening or screaming at the adversary, but can also be accomplished by approaching or shrinking back into contact with a potential supporter whilst lipsmacking toward the latter. (Threats and screams given by participants in a conflict can also function to draw the attention of others and recruit support, but were specified separately and were not subsumed under the behaviour pattern *enlist*).

*General enlist* Repeated scanning of the vicinity using headflagging motions during an ongoing aggressive interaction, often whilst vocalizing (threatening or screaming) toward the opponent, in an apparent search for potential supporters. This is distinguished from an *enlist* (above), by the fact that these actions are not directed toward a specific individual or individuals.

*Coalition* To actively support (via aggressive actions) an individual or faction aggressing against, or receiving aggression from, a third party (or parties). Also covers instances where two individuals simultaneously and jointly commence aggression against a third. Any solicitation behaviour by either side, the order of entry of individuals into the conflict, the party assisted, and whether the intervention prompted the target to submit or cease aggression would additionally be specified.

*Help* To join in an ongoing aggressive interaction between others, but without using any overt aggression. The helper typically approaches and *screams* or *alarm barks* at the aggressor whilst frantically *general enlisting*, or may dash or *lunge* at the aggressor whilst simultaneously *screaming* loudly. Such interventions are always in favour of the victim of the original conflict, in cases where the helper itself is

also lower-ranking than the aggressor, and can successfully divert the aggressor's attention away from the victim (often towards the helper itself).

*Passive support* Participation in an imminent or ongoing aggressive confrontation by directing an affiliative act toward one contestant, usually the aggressor. Observed only in immature individuals, often males. The third party (which typically outranks the beneficiary, and often the opponent as well) approaches and either places an arm around the shoulders of and stands in contact with the beneficiary, or mounts the latter, whilst intently watching the opponent in an intimidatory fashion. This behaviour seems to encourage the beneficiary to commence aggression or intensify its aggressive efforts.

*Approach scene* To approach to within 5 metres (the exact distance being specified as either ≤0.6m, ≤2m or ≤5m) of an ongoing conflict, but without actively intervening in any way. Sometimes exhibited by high-ranking relatives or allies of a contestant which appeared to simply monitor the situation, but more usually seen in potential supporters of the victim which appear distressed but unable to overtly intervene due to their being much lower-ranking than the aggressor.

*Aggression between others* To provide a measure of "opportunity" to interfere in the conflicts of others, overt aggression occurring between third parties in the vicinity (≤10m radius) of the focal subject was systematically recorded. Interactions were scored only if they were of at least lunge intensity (see the hierarchy of aggressive acts provided above), and/or if accompanied by agonistic vocalizations by either party, to ensure that all such occurrences were likely to be noticed and thus systematically recorded. Details noted included the number and identity of participants on each side, and distance from the focal (assigned as either ≤5m or ≤10m).

## *Sexual interactions*

*Muzzle up* Puckering facial expression made by males when approaching and soliciting copulation from females. The lips are compressed and protruded, whilst eyebrows, forehead and ears are retracted, and with the head tilted back so that the chin is thrust upwards.

*Genital inspect*† Olfactory, oral or manual examination of another individual's genital area.

*Slap ground* To strike the ground with the palm of the hand, usually in a somewhat agitated manner. Performed by a mating female, perhaps to encourage a *mount* sequence.

*Hip push* To briefly push another individual's pelvis with one or both hands, encouraging the recipient to stand for a *mount*.

*Present (sexual)* A proceptive display in which a standing female presents her hindquarters to a male, sometimes accompanied by leg flexure and glancing back over the shoulder towards the recipient.

*Mount (sexual)*† Alignment of the male's hindquarters with the haunches of the female, usually with hands grasping the recipient's waist or hips, and with the actor's feet either grasping the recipient's calves or remaining on the ground. The following subcategories were distinguished: [1] Mount without obvious intromission, with or without pelvic thrusting. [2] Mount involving intromission and pelvic thrusting. [3] As for the previous category, but with either an ejaculatory pause by the male, or evidence of fresh ejaculate on the recipient's perineum or the actor's scrotum. Duration was only recorded if the mount lasted ≥5 seconds.

*Reach back* A clutching reaction made by females whilst being mounted, involving twisting back to grab and pull on the male's leg, scrotum or tail.

*Grind teeth* Rubbing of the lower teeth against the upper set, producing a quiet grinding or screeching sound. Observed in males during copulation.

*Copulation call* Loud call (similar to a soft scream) given by males while thrusting during a mount series when near ejaculation, or while dismounting. Accompanied by retraction of the lips, but with the teeth clamped shut.

*Masturbate*† Males: Repeated manual stimulation of the penis, sometimes culminating in ejaculation; females (occasionally): rubbing the ano-genital region back and forth against a hard substrate, usually a branch. This behaviour was not scored unless a minimum duration of ≥5 seconds was achieved.

*Self-inspect*† Manual examination of own ano-genital region, in females occasionally followed by olfactory inspection of the hands. May occur embedded within a wider *self-grooming* bout. This behaviour was not scored unless a minimum duration of ≥5 seconds was achieved.

## *Miscellaneous social behaviour*

The following behaviour patterns were used in diverse social contexts:

*Approach* Movement to within arm's reach (≤0.6m) of another individual, if the approacher remained within this range for ≥5 seconds, or if followed by a more overt interaction between the two animals. If the recipient was in possession of and/or using a resource, this would also be noted. Approaches were not scored if both individuals were travelling. For the purposes of recording interactions which commenced when an individual approached to a point more distant than 0.6m, the distance (m) would be recorded as part of a *long approach*, although this type of approach was not continuously recorded in the absence of any overt interaction.

*Leave* Moving beyond arm's reach (>0.6m) of another individual, after an interaction or after an approach of ≥5s duration. A *long leave* (m) would be recorded if an interaction took place between two individuals which had been more widely separated.

*Pass past* To walk obliquely past another individual without stopping, at a specified distance (m). Only noted in the continuous data when the actor either signalled to, or its movement provoked a response by, the recipient.

*Follow* Movement in order to maintain proximity to another individual, if clearly directed and initiated within ≤10 seconds of the target's departure beyond a former separation of ≤2m.

*Restrain*† Preventing a smaller individual (usually an infant) from moving away by holding onto its limb(s) or tail. Used by mothers to prevent infants from straying near situations apparently perceived as dangerous, and by juveniles attempting to continue affiliation with reluctant partners.

*Resist* Attempts, successful or otherwise, to free oneself from the grasp of another individual, whether in an affiliative (e.g. in response to a play attempt) or an assertive (e.g. when being held down by another) context.

*Ignore* To fail to respond to another's affiliative or agonistic overtures in situations where the actor appeared fully aware of the latter. In some cases involved conspicuously turning the body to face away from, and thereby cut off, the interactant.

*Glance* To look at another individual briefly (typically <3 seconds). Only scored when pertinent to a sequence of more overt interactions.

*Present* Orienting the hindquarters toward another individual, with semi-rigid stance. Gesture which occurs in diverse contexts and may serve as an appeasement or greeting gesture, or preceding affiliation. The lesser degree of leg flexure and spinal curvature, type of orientation toward, and glancing at, the recipient can often be used to distinguish submissive and affinitive versions from *sexual presents*, together with the context in which the act is performed.

*Freeze* To temporarily cease an ongoing activity (e.g. grooming of a third party) in response to the *approach* or *passing past* of another (more dominant) individual.

*Startle* A sudden whole-body start, as if in deflection from a falling object. Typically occurs in response to a sudden noise, or the unexpected appearance of another individual.

*Display* Bouncing upon substrate with stiff limbs or manually shaking objects or substrate (e.g. branches) to create a drumming sound, often in a somewhat intimidatory fashion. Typically performed by males, and may or may not be "directed" toward a particular witness. Identity of, and distance to, the nearest individual was also noted.

*Alarm bark* A loud, repeated and sharp sounding vocalization, functioning to alert conspecifics to the presence of potential predators or dangerous situations. In this population the call can be elicited by turkey vultures, unfamiliar humans, machinery or capture nets.

*Whoo call* Drawn out, conspicuous and harmonically rich distress call, typically given repeatedly when separated from social companions, and accompanied by climbing of vantage points and scanning of surroundings. Produced with fairly widely separated lips, protruded to form a distinct "0"-shape. Similar calls are produced when foraging or waiting for chow to be placed in dispensers, and during group progression. These "coo" calls appear to function in maintaining contact between spatially dispersed group members, particularly kin or others which have recently been involved in affiliative interactions.

*Chorus* A seemingly contagious vocalization resembling either a *low grunt* or *vocal threat*, depending upon whether the predominant mood of the participants appeared affiliative or aggressive (in the latter case typically occurring as a prelude to coalition formation, or after a multipartite aggressive event has subsided). Often initiated by an individual which vocalizes while moving excitedly between other group members, which then also vocalize. Function unknown.

*Gecker* Short rapid bursts of an abrupt and relatively low-pitched hacking vocalization, sometimes accompanied by spasmodic jerking of the body, or even a full-blown *temper tantrum* (see below). Given by infants and young juveniles, usually when prevented from suckling, pushed away from social contact or prevented from obtaining an apparently desired resource, or when subjected to *rough behaviour*.

*Temper tantrum* Repeated violent spasmodic movements of the limbs and body, this flailing culminating by clinging tightly to the mother or social partner or, in extreme cases, by crouching face down against the ground. Almost always accompanied by *geckers* or *screams*. Given by infants and young juveniles, protesting when prevented from suckling or when pushed away from social contact.

## *Self-directed behaviour*

*Scratch* A usually repeated movement of the hand or foot, during which the digital tips are rapidly raked across the individual's hair or skin.

*Bodyshake* A shaking movement of the entire body, with torso rotating around the axis of the spine, and apparently most vigorous in the shoulder region (posture and motion being similar to that of a wet dog).

*Yawn* A brief gaping movement of the mouth, in which the canine teeth may be exposed. Performed in a variety of contexts, including when resting or falling asleep, in tense situations, and in males some instances possibly involve a mild threat display.

*Self-groom*$^{\dagger}$ Picking through and/or slowly brushing aside an individual's own hair or skin, using one or both hands and/or the mouth. This behaviour was not scored unless a minimum duration of ≥5 seconds was achieved.

The following additional behaviour patterns were scored only during instantaneous (point) time samples. Categories of behaviour were employed hierarchically in the order of precedence Social > Feed > Locomotion > Self- or object-directed > State, such that the classification "state" was usually utilised only where no higher category applied. However where a subject was engaged in vocalizing, feeding, self- or object-directed behaviour, chewing food from cheek pouches, or was asleep, whilst also engaged in a higher category of act (for example sitting in contact with another individual) then the secondary activity would also be noted.

## *PTS: Social*

*Includes* For this purpose includes ongoing involvement in any of the social interactions listed previously (Affiliative, Agonistic, Sexual), as well as those listed under Miscellaneous acts.

*Watch other* Attention intently focused upon a particular conspecific. The identity of this individual, and its activity and distance (m) to the subject would also be recorded.

## *PTS: Feed*

*Forage* Preparing or ingesting any naturally occurring food item, including vegetation, digging and eating soil from habitually used dips in the ground, searching for and consuming small invertebrates. The type and part of the matter ingested would additionally be specified (e.g. leaves, bark, roots, buds, flowers, coconut, sea grasses, soil, insects, etc.).

*Chow* Procuring, handling (e.g. washing) or consumption of protein biscuits.

*Drink* Drinking water from a fountain or pool, or licking rainwater from leaves or small crevices. The source would be specified.

## *PTS: Locomotion*

Travel through the environment, when not integral to performance of a social activity or feeding, was specified as either *walk*, *run*, *jump*, *climb* or *swim* (all definitions as in common usage).

## *PTS: Self-directed behaviour*

*Includes* All behaviours specified under this heading, above.

## *PTS: Object- or environment-oriented behaviour*

*Manipulate* Repeated handling, turning over or rubbing of small objects such as twigs and stones, or swift sweeping movements back and forth across the surface of leaf litter or soil, performed in a non-feeding context. Occasionally involves rubbing the hands up and down a larger object such as a tree trunk. The movements are often performed in a somewhat distracted or "fidgety" fashion.

*Gnaw* Repeated gentle mouthing and/or scraping of one's teeth across a hard object such as a branch, stone or coconut husk, performed without ingesting the substrate and not as part of a foraging bout. The subject typically is not attending to the object concerned, instead monitoring a conspecific or glancing around the environment. This behaviour category also included repeatedly rubbing one's face back and forth against objects such as tree trunks.

*Solitary play* Stationary or locomotor play usually incorporating the handling of objects, when performed without a partner. Examples include prancing and cartwheeling while dragging - or grasping in the mouth and shaking head from side to side - objects such as leafy branches or coconut husks; swinging back and forth from llianas, often while upside-down; repeatedly jumping ("bombing") into pools of water.

*Visual scan* Rapid scrutinising of the surroundings, involving head-turning of at least 180° in one continuous motion or rapid sequential glances to different parts of the environment.

## *PTS: State*

*Cheek pouch* Consuming food held within the cheek pouches (forage versus chow were specified where possible), but not actively feeding.

*Watch object* Stationary, with attention intently focused upon a specified object in the environment.

*Alert* Stationary, with attention not focused upon any particular point in the environment, but visual checking of surroundings has occurred within the 5 seconds preceding the point time sample.

*Rest* Stationary and clearly relaxed, with eyes open but oriented in a downward manner, or alternately open and closed; no visual checking of surroundings in the 5 seconds preceding the point time sample.

*Sleep* Common usage i.e. stationary with eyes closed, and slow and regular breathing.

This ethogram was developed during a period of data collection at Cayo Santiago prior to this study, and owes much to previously published ethograms by Altmann (1962) and Hinde & Rowell (1962), in which the main affiliative and agonistic behaviour patterns are well covered. For more detailed descriptions of particular entries, the following publications should prove useful. Symons (1978) provides a review of play postures and signals in rhesus macaques, while sexual and sociosexual behaviour patterns are covered in more detail by Dixson (1998). Further description of the predominant facial and gestural signals used by rhesus macaques are provided by van Hooff (1962), de Waal & Luttrell (1985) and Maestripieri & Wallen (1997), while descriptions, contextual usage and/or spectrograms of the vocal repertoire can be located in Rowell & Hinde (1962), Rowell (1962), Gouzoules *et al.* (1984), Hauser (1991), Hauser & Marler (1993), Rendall *et al.* (1996), Silk *et al.* (2000), and are reviewed by Hauser (1996).

# *Appendix C*

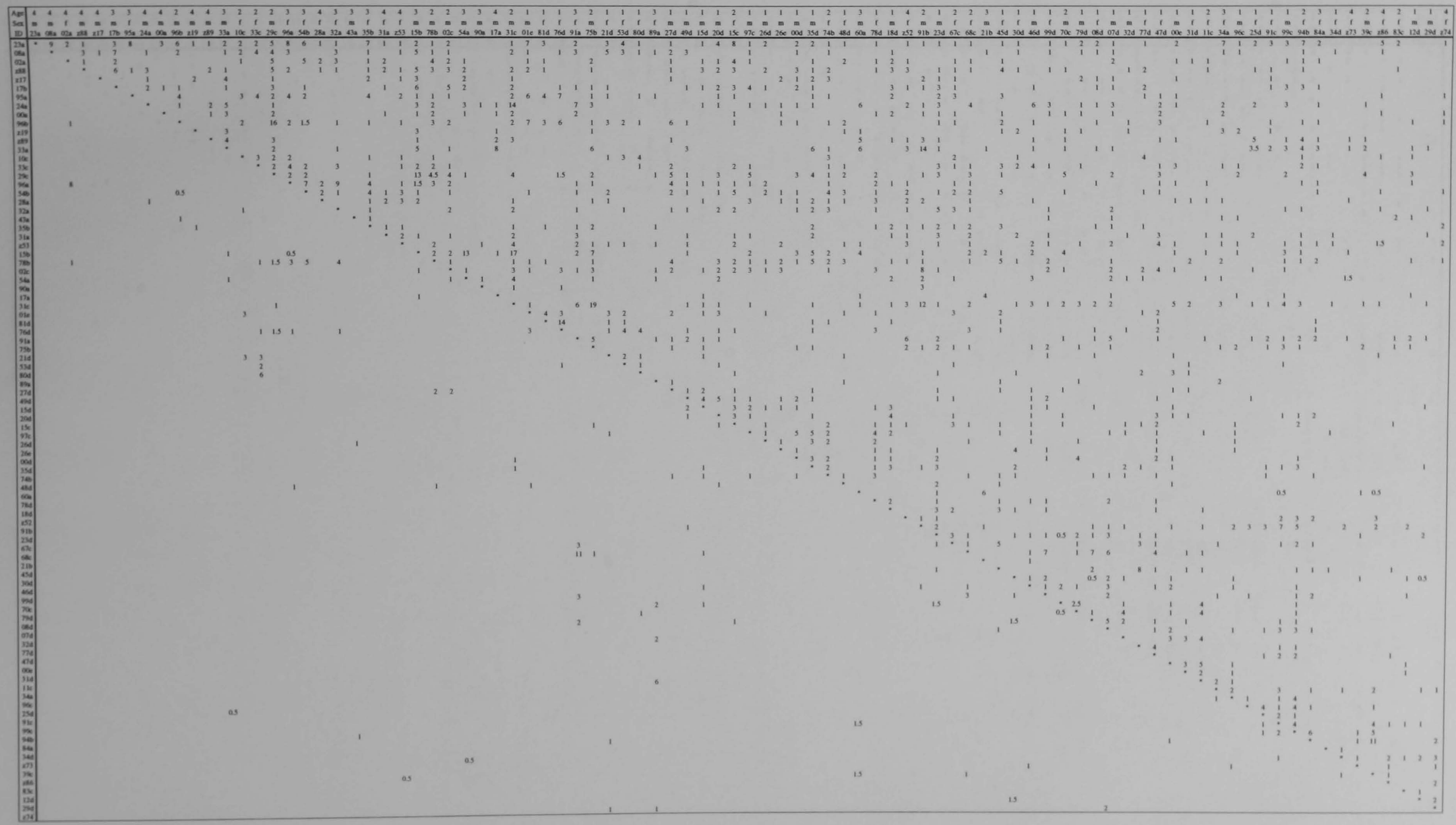
## *Summary of additional conflicts and post-conflict intervals extracted from 30-minute focal observations and used in post-conflict analyses.*

Conflicts are defined as agonistic interactions involving at minimum a threat display. Details provided refer only to the subset of "marker" conflicts followed by a continuous 10-minute period of observation. Analyses requiring shorter post-conflict intervals are based upon a greater proportion of the total conflicts observed. Further details of subject and conflict selection are provided in chapter 2.

| Subject | Age | Sex | Group | Maternal rank | Subject rank | Minutes observed | Total conflicts | Marker conflicts | By role in conflict: Aggr | Victim | Bidi | Conflict type: Dyadic | Polyadic |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 01e | 1 | M | R | 1 | 32 | 720 | 28 | 11 | 5 | 5 | 1 | 9 | 2 |
| 35d | 1 | M | R | 1 | 50 | 720 | 32 | 10 | 4 | 6 | 0 | 8 | 2 |
| 23d | 1 | M | R | 2 | 58 | 720 | 35 | 19 | 4 | 14 | 1 | 17 | 2 |
| 00e* | 1 | M | R, BB | 2 | 73, 25 | 720 | 42 | 14 | 1 | 13 | 0 | 12 | 2 |
| 14d | 1 | M | BB | 3 | 21 | 720 | 38 | 14 | 3 | 11 | 0 | 11 | 3 |
| 02e | 1 | M | BB | 3 | 33 | 720 | 19 | 9 | 0 | 9 | 0 | 6 | 3 |
| 21d | 1 | F | R | 1 | 37 | 720 | 20 | 12 | 3 | 9 | 0 | 9 | 3 |
| 78d | 1 | F | R | 1 | 54 | 720 | 24 | 11 | 5 | 5 | 1 | 7 | 4 |
| 45d | 1 | F | R | 2 | 62 | 720 | 25 | 3 | 0 | 3 | 0 | 2 | 1 |
| 47d | 1 | F | R | 2 | 72 | 720 | 42 | 20 | 3 | 15 | 2 | 16 | 4 |
| 75d | 1 | F | BB | 3 | 16 | 720 | 31 | 9 | 7 | 1 | 1 | 5 | 4 |
| 51d | 1 | F | BB | 3 | 34 | 720 | 30 | 14 | 1 | 12 | 1 | 12 | 2 |
| 02c* | 2 | M | R | 1 | 27 | 720 | 31 | 11 | 5 | 6 | 0 | 9 | 2 |
| 29c | 2 | M | R | 1 | 16 | 720 | 29 | 13 | 6 | 5 | 2 | 11 | 2 |
| 78b | 2 | M | R | 1 | 26 | 720 | 23 | 11 | 4 | 5 | 2 | 7 | 4 |
| 31c | 2 | M | R | 2 | 31 | 720 | 44 | 15 | 7 | 8 | 0 | 12 | 3 |
| 32c | 2 | M | BB | 3 | 30 | 720 | 44 | 16 | 2 | 14 | 0 | 13 | 3 |
| 91b | 2 | M | R | 3 | 57 | 720 | 25 | 10 | 4 | 5 | 1 | 8 | 2 |
| 33c | 2 | F | R | 1 | 15 | 720 | 38 | 12 | 3 | 9 | 0 | 10 | 2 |
| 15c | 2 | F | R | 1 | 45 | 720 | 30 | 13 | 1 | 10 | 2 | 9 | 4 |
| 68c | 2 | F | R | 2 | 60 | 720 | 25 | 13 | 3 | 9 | 1 | 7 | 6 |
| 11c | 2 | F | R, BB | 2 | 75, 9 | 720 | 41 | 13 | 6 | 6 | 1 | 6 | 7 |
| 93b | 2 | F | BB | 3 | 20 | 720 | 36 | 13 | 8 | 4 | 1 | 10 | 3 |
| 94b | 2 | F | R | 3 | 81 | 720 | 36 | 14 | 2 | 9 | 3 | 9 | 5 |
| 17b | 3 | M | R | 1 | 6 | 720 | 41 | 13 | 8 | 4 | 1 | 9 | 4 |
| 15b | 3 | M | R | 1 | 25 | 720 | 44 | 17 | 8 | 8 | 1 | 10 | 7 |
| 54a | 3 | M | R, F | 2 | 28 | 480 | 20 | 6 | 1 | 5 | 0 | 5 | 1 |
| 85a | 3 | M | BB | 2 | 3 | 720 | 41 | 11 | 6 | 2 | 3 | 4 | 7 |
| 49a | 3 | M | BB | 3 | 4 | 720 | 37 | 11 | 2 | 8 | 1 | 9 | 2 |
| 33a* | 3 | M | R | 3 | 13 | 720 | 44 | 16 | 7 | 9 | 0 | 13 | 3 |
| 95a | 3 | F | R | 1 | 7 | 720 | 32 | 14 | 9 | 4 | 1 | 11 | 3 |
| 35b* | 3 | F | R | 1 | 22 | 720 | 34 | 11 | 7 | 4 | 0 | 11 | 0 |
| 91a | 3 | F | R | 2 | 35 | 720 | 51 | 20 | 8 | 12 | 0 | 17 | 3 |
| 37b | 3 | F | BB | 2 | 1 | 720 | 29 | 16 | 7 | 8 | 1 | 12 | 4 |
| 93a | 3 | F | BB | 3 | 24 | 360 | 17 | 6 | 1 | 5 | 0 | 6 | 0 |
| 52a | 3 | F | BB | 3 | 27 | 360 | 22 | 6 | 0 | 6 | 0 | 5 | 1 |
| 34a | 3 | F | R | 3 | 76 | 720 | 22 | 15 | 9 | 6 | 0 | 11 | 4 |

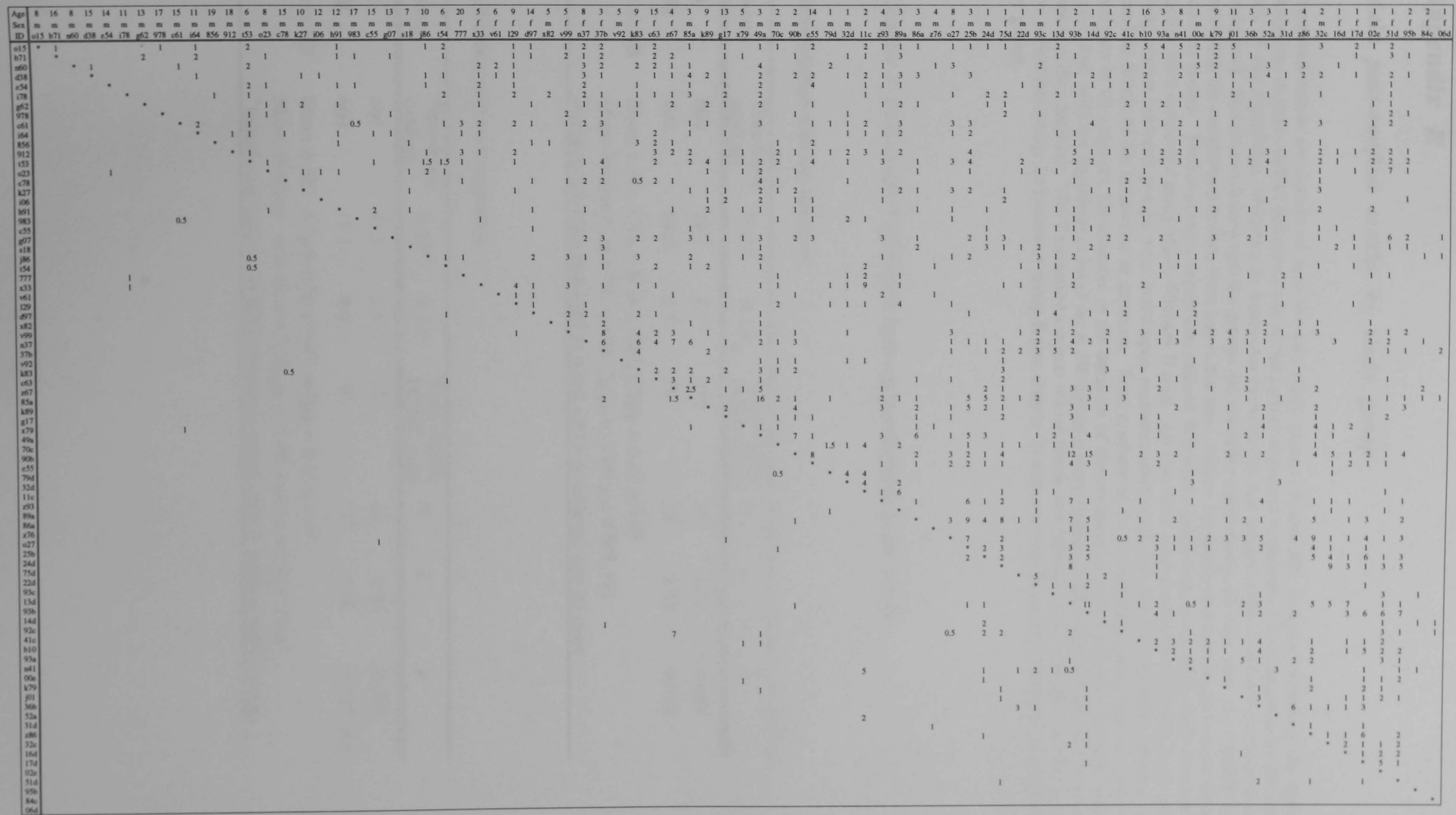
*Group*: two groups given for subjects which transferred between groups R and BB during study period, and one subject's natal emigration; predominant affiliation is placed first. *Maternal rank*: subject selection was based upon mother's position in the adult female hierarchy (1=upper, 2=middle, 3=lower third) in the pre-fission group R. *Subject rank*: Juvenile's own position within respective (post-fission) study group; two positions given for subjects which transferred between groups R and BB. *Minutes observed*: total sampling time was reduced due to natal emigration (54a) or death of subject (52a); latter was replaced for remainder of study by (93a). *Subject orphaned before or partway through study.

# *Appendix D1. Dominance hierarchy for immature members of group R, March - December 1996*



Based upon *ad libitum* observations of agonistic interactions, with individual on vertical axis scored as winner. Numbers refer to dyadic totals of observed interactions; 0.5 values refer to aggressive interactions with undecided outcome. Due to space constraints, only interactions pertaining to 1-4 year old group members are displayed.

# *Appendix D2. Dominance hierarchy for group BB, March - December 1996*



Based upon *ad libitum* observations of agonistic interactions, with individual on vertical axis scored as winner.
Numbers refer to dyadic totals of observed interactions; 0.5 values refer to aggressive interactions with undecided outcome.

# *Appendix E*

## *Main post-conflict results by study group*

Presented below are details of how the two study groups, R and BB, compare regarding the main categories of post-conflict behaviour and social partner examined in chapters 3-6, illustrating the general lack of any significant difference in behaviour between the two groups when direct comparisons were performed. Before concluding that the groups did not differ significantly, all tests were also checked by restricting the comparison to data from any initial time window applicable and subjects possessing more accurate scores. Within-group comparisons utilised Wilcoxon-signed ranks tests, while those between-groups were conducted using Mann-Whitney *U* tests. All tests were conducted at the individual level, and comparisons between groups were based upon measures which took into account potential variation in baseline levels of the behaviour in question. Tests conform to the format followed in specific chapter analyses in all respects, for example in the duration of the observation period utilised. All tests were two-tailed, with the significance level set at 5% unless a more rigorous alpha criterion was in operation (see specific chapters). The 7 immature subjects whose family had transferred between the two groups in the period following the fission of group R (see chapter 2) were necessarily excluded from these analyses by group.

### *Chapter 3: Post-conflict affiliation between participants in the conflict*

Reconciliation with any opponent:

| Group | Time-frame used/ sec | % EP | % LP | Total eligible PC/MC pairs | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|---|
| R | 600 | 19.7 | 2.7 | 335 | 75 | -4.41 | 0.000 |
| BB | 600 | 19.0 | 2.5 | 79 | 25 | -2.58 | 0.010 |
| R vs BB | Mean ± SE: $CT_R = 0.18 \pm 0.04$, $CT_{BB} = 0.20 \pm 0.07$ | | | | | | |
| | Mann-Whitney: $m = 75$, $n = 25$, $Z_{corr} = -0.05$, $p = 0.964$, NS | | | | | | |
| | Remains NS when restricted to initial <200s & subjects with ≥3 pairs | | | | | | |

Affiliation with own supporters:

| Group | Time-frame used/ sec | % EP | % LP | Total eligible PC/MC pairs | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|---|
| R | 600 | 45.5 | 2.6 | 77 | 48 | -4.54 | 0.000 |
| BB | 600 | 11.1 | 0.0 | 9 | 7* | -1.00 | 0.317, NS |
| R vs BB | Mean ± SE: $AT_R = 0.50 \pm 0.07$, $AT_{BB} = 0.14 \pm 0.14$ | | | | | | |
| | Mann-Whitney: $m = 48$, $n = 7$, $Z_{corr} = -1.86$, *exact* $p = 0.094$, Trend | | | | | | |
| | *Insufficient subjects in BB to restrict to initial <60s & subjects with ≥2 pairs | | | | | | |

## *Chapter 4: Consequences of involvement in aggression*

Mean scratching bouts/ min in post-conflict observations without reconciliation or aggression initiated against bystanders, versus matched-control observations:

| Group | Time-frame used/ sec | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| R | 600 | 0.29 ± 0.04 | 0.16 ± 0.02 | 68 | -3.97 | 0.000 |
| BB | 600 | 0.24 ± 0.04 | 0.15 ± 0.02 | 21 | -1.73 | 0.084, Trend |
| R vs BB | (Mean PC - mean MC) bouts/ min: R = 0.14 ± 0.04, BB = 0.09 ± 0.05<br>Mann-Whitney: *m* = 68, *n* = 21, *Zcorr* = -0.59, *p* = 0.558, NS | | | | | |

Mean bouts/ min of aggression received in post-conflict observations without reconciliation or aggression initiated against bystanders, versus matched-control observations:

| Group | Time-frame used/ sec | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| R | 420 | 0.05 ± 0.007 | 0.03 ± 0.005 | 68 | -1.28 | 0.200, NS |
| BB | 420 | 0.06 ± 0.021 | 0.02 ± 0.006 | 21 | -2.23 | 0.026 |
| R vs BB | (Mean PC - mean MC) bouts/ min: R = 0.02 ± 0.009, BB = 0.05 ± 0.023<br>Mann-Whitney: *m* = 68, *n* = 21, *Zcorr* = -1.26, *p* = 0.208, NS | | | | | |

Mean proportion of time spent feeding in post-conflict observations without reconciliation or aggression initiated against bystanders, versus matched-control observations:

| Group | Time-frame used/ sec | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| R | 600 | 0.20 ± 0.022 | 0.28 ± 0.025 | 68 | -2.65 | 0.008 |
| BB | 600 | 0.20 ± 0.036 | 0.31 ± 0.049 | 21 | -1.77 | 0.077, Trend |
| R vs BB | (Mean PC - mean MC) propn: R = -0.08 ± 0.030, BB = -0.11 ± 0.056<br>Mann-Whitney: *m* = 68, *n* = 21, *Zcorr* = -0.24, *p* = 0.812, NS | | | | | |

Mean proportion of time spent in locomotion in post-conflict observations without reconciliation or aggression initiated against bystanders, versus matched-control observations:

| Group | Time-frame used/ sec | PC mean ± SE | MC mean ± SE | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|
| R | 600 | 0.15 ± 0.013 | 0.11 ± 0.010 | 68 | -2.59 | 0.010 |
| BB | 600 | 0.18 ± 0.027 | 0.11 ± 0.018 | 21 | -2.07 | 0.038 |
| R vs BB | (Mean PC - mean MC) propn: R = 0.05 ± 0.016, BB = 0.07 ± 0.029<br>Mann-Whitney: *m* = 68, *n* = 21, *Zcorr* = -0.66, *p* = 0.509, NS | | | | | |

## *Chapter 5: Post-conflict affiliation with third parties*

Affiliation with own kin bystanders:

| Group | Time-frame used /sec | *N* | *Z* | *p* |
|---|---|---|---|---|
| R | 600 | 67 | -4.40 | 0.000 |
| BB | 600 | 24 | -1.02 | 0.309, NS |
| | 110 | 24 | -1.73 | 0.084, Trend |
| R vs BB | Mean ± SE: $AT_R = 0.27 \pm 0.05$, $AT_{BB} = 0.12 \pm 0.12$ | | | |
| | Mann-Whitney: $m = 67$, $n = 24$, $Z_{corr} = -1.13$, $p = 0.259$, NS | | | |
| | Remains NS when restricted to initial <110s & subjects with ≥3 pairs | | | |

Affiliation with initial opponent's kin bystanders:

| Group | Time-frame used /sec | *N* | *Z* | *p* |
|---|---|---|---|---|
| R | 600 | 71 | -2.97 | 0.003 |
| BB | 600 | 24 | -1.75 | 0.080, Trend |
| | 110 | 24 | -1.13 | 0.260, NS |
| R vs BB | Mean ± SE: $AT_R = 0.14 \pm 0.05$, $AT_{BB} = 0.21 \pm 0.11$ | | | |
| | Mann-Whitney: $m = 71$, $n = 24$, $Z_{corr} = -0.66$, $p = 0.511$, NS | | | |
| | Remains NS when restricted to initial <110s & subjects with ≥3 pairs | | | |

## *Chapter 6: Aggression initiated against third parties*

Aggression initiated against bystanders by former aggressors:

| Group | Time-frame used/ sec | % EP | % LP | Total eligible PC/MC pairs | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|---|
| R | 600 | 30.5 | 12.7 | 118 | 49 | -2.44 | 0.015 |
| BB | 600 | 40.0 | 8.0 | 25 | 13 | -2.20 | 0.028 |
| R vs BB | Mean ± SE: $AT_R = 0.17 \pm 0.07$, $AT_{BB} = 0.33 \pm 0.12$ | | | | | | |
| | Mann-Whitney: $m = 49$, $n = 13$, $Z_{corr} = -0.96$, $p = 0.339$, NS | | | | | | |
| | Remains NS when restricted to initial <130s & subjects with ≥2 pairs | | | | | | |

Aggression initiated against bystanders by former victims:

| Group | Time-frame used/ sec | % EP | % LP | Total eligible PC/MC pairs | *N* | *Z* | *p* |
|---|---|---|---|---|---|---|---|
| R | 600 | 34.8 | 8.5 | 141 | 61 | -4.01 | 0.000 |
| BB | 600 | 21.6 | 10.8 | 37 | 21 | -0.94 | 0.347, NS |
| | 130 | 13.2 | 5.3 | 38 | 21 | -1.44 | 0.151, NS |
| R vs BB | Mean ± SE: $AT_R = 0.29 \pm 0.06$, $AT_{BB} = 0.11 \pm 0.12$ | | | | | | |
| | Mann-Whitney: $m = 61$, $n = 21$, $Z_{corr} = -1.32$, $p = 0.185$, NS | | | | | | |
| | Remains NS when restricted to initial <130s & subjects with ≥2 pairs | | | | | | |